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Distribution and Survival of Herring Larvae (*Clupea pallasi* Valenciennes) in British Columbia Waters[1, 2]

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ABSTRACT

Through study of the distribution and survival of herring larvae of one of the main populations in British Columbia waters, it is concluded that (a) the principal cause of death in Pacific herring larvae is traceable to their passive transport by inshore water currents to the open sea, and (b) the number of larvae that are not so transported in any particular year determines the strength of the resulting year-class.

Greatest concentration of larvae after hatching was found in inshore waters near the spawning grounds, and as they were carried seaward the numbers remaining decreased at an approximately constant rate. The movement of larvae, as noted through sampling, was related to the pattern of water currents, as determined by oceanographic survey. The extensive movement of larvae offshore was explained through seaward moving currents being strongest (a) in waters in which the largest larval broods were present, and (b) at the surface of the water where larvae were heavily concentrated at night. Predation, lack of food, and conditions of temperature and salinity were not considered important mortality factors in inshore areas.

Sampling indicated that few larvae carried to sea returned to inshore waters. Furthermore, several pieces of evidence suggested that most larvae carried offshore did not survive. The failure to find either larvae offshore or nearly-metamorphosed juveniles near the mouth of Barkley Sound appeared significant, particularly since schools of the latter were regularly found inshore near the spawning grounds. The factors directly causing death in offshore waters were not determined, but it was suggested that death may be connected with the high salinity of the open sea. It was concluded that the strength of herring year-classes was largely determined by the numbers of larvae that remained in inshore waters during the critical period of larval life.

Meteorological factors were considered capable of causing annual variations in current flow and hence in year-class strength, and the delayed effect of snow on river discharge appeared to be of greater importance than the more immediate effect of rainfall. No single meteorological factor, however, seemed to have a dominant influence.

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[2] Based on a thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy at the University of Toronto.

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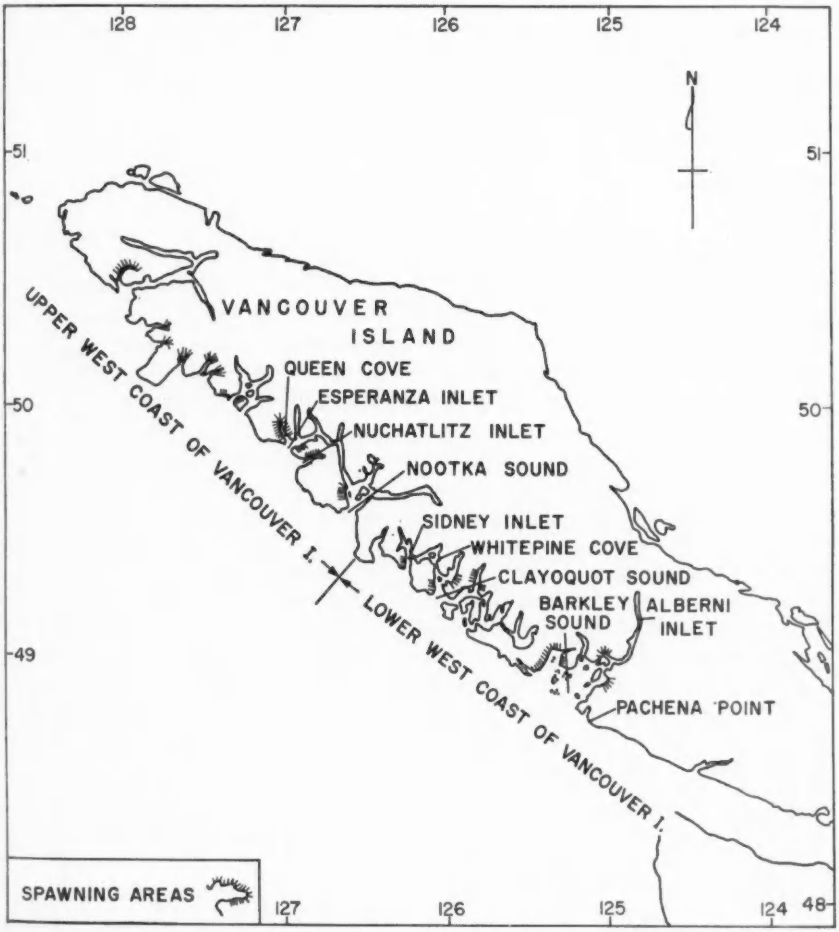
INTRODUCTION

DURING THE PAST 40 YEARS much research has been devoted to factors affecting the survival of marine fish. Probably no species has been subjected to more investigation of this type than the Atlantic herring. The more significant herring studies include those of Wallace (1924), Johansen (1924), Lissner (1927), Schnakenbeck (1927), Tesch (1929), Mielck (1929), Altnöder (1929) and Büchmann (1950a), in which the movements of larvae were followed from the spawning grounds in the North Sea and were related to ocean currents. On the basis of these investigations wide acceptance has been gained for the view (stated generally by Hjort, 1914) that the most critical period for herring survival is during larval life when the larvae are being passively transported in ocean currents. There is, however, little evidence on what the specific mortality factors are and how they operate during this critical period.

In this paper the writer reports on a study of Pacific herring larvae (*Clupea pallasi* Valenciennes) in British Columbia waters carried out from 1947 to 1951 in an attempt to determine the factors responsible for causing variations in the strength of year-classes. These studies were mainly concerned with the herring population of the lower west coast of Vancouver Island (Fig. 1), one of the 8 more or less discrete stocks of the British Columbia coast (Stevenson, 1955a), and more particularly with the larvae derived from spawnings in the northern part of Barkley Sound where about three-quarters of the spawning of this population occurs (Tester and Stevenson, 1947, 1948; Stevenson, 1950; Stevenson and Lanigan, 1950; Stevenson *et al.*, 1951; Stevenson *et al.*, 1952).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VANCOUVER ISLAND
QUEEN COVE
ESPERANZA INLET
NUCHATLITZ INLET
NOOTKA SOUND
SIDNEY INLET
WHITEPINE COVE
CLAYOQUOT SOUND
BARKLEY SOUND
ALBERNI INLET
PACHENA POINT
UPPER WEST COAST OF VANCOUVER I.
LOWER WEST COAST OF VANCOUVER I.
SPAWNING AREAS

FIG. 1. Map of the west coast of Vancouver Island showing location of the main herring spawning grounds and identifying certain place-names mentioned in the text. For detail of Barkley Sound, see Fig. 11.

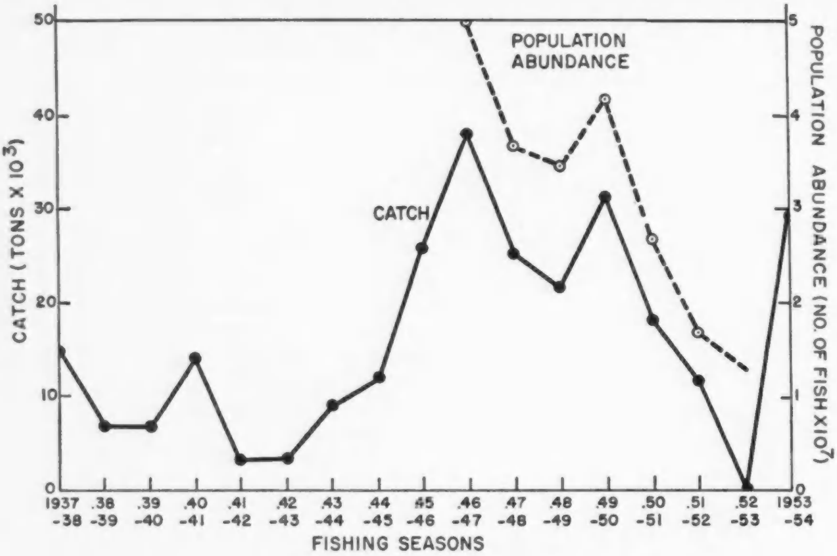

FIG. 2. Catch of herring on the lower west coast of Vancouver Island in fishing seasons from 1937–38 to 1953–54, with estimated population abundance in fishing seasons 1946–47 to 1952–53.

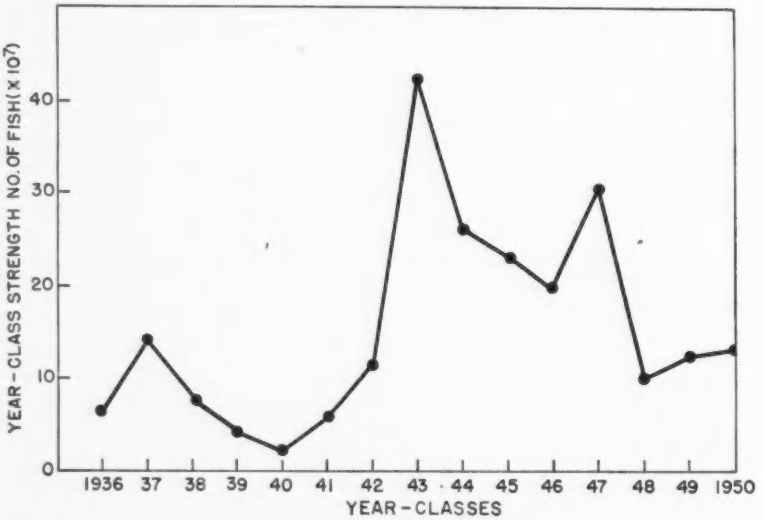

FIG. 3. Relative strength of the year-classes 1936 to 1950 in the herring population of the lower west coast of Vancouver Island.

The Pacific herring in British Columbia waters spawns in late winter and early spring in shallow water near shore, mostly on fixed vegetation within the intertidal zone. After spawning the spent fish move offshore and feed in the surface waters of the Continental shelf, returning to inshore waters as compact schools during the fall and winter months, at which time the fishery occurs. The eggs hatch in about 2 weeks into elongate, semi-transparent larvae which float passively in the water, and after 4 to 6 weeks the body shape changes to resemble that of the adult. After this "metamorphosis", the larvae cease to exist as free-floating organisms and form schools which appear in the vicinity of the spawning grounds (Stevenson, 1947). During the first summer, the young (juveniles) stay in inshore waters and concentrate in areas of relatively low salinity (Hourston, 1959). In the fall and winter they disappear from inshore waters but reapper inshore during their second summer as schools of immature fish. The main recruitment to the mature stocks occurs in the third year, at which time about four-fifths of the year-class enters the fishable stocks (Stevenson, 1955b).

Variations in the commercial catch during the period 1937-38 to 1953-54 (Fig. 2) on the lower west coast of Vancouver Island are considered to reflect changes in population abundance (Appendix 1), and on this basis relative year-class strength (Fig. 3) is calculated using methods described in Appendix 2.

A review of pertinent evidence of Fraser (1916), Hubbs (1925), Schnakenbeck (1931), Rass (1939), Tester (1946), Berg (1948), and Ekman (1953), has led the writer to take the view that the Pacific herring (*Clupea pallasi* Valenciennes) and the Atlantic herring (*C. harengus* L.) are conspecific, according to Mayr's (1942) definition. On this basis extensive comparison is made in this paper of the behaviour of Pacific and Atlantic herring larvae. The most noteworthy difference in behaviour concerns the locality of spawning. While the Pacific herring spawn mainly within or just below the tidal zone in water of relatively low salinity, the Atlantic herring spawn at greater depths, frequently at a distance from shore in water of high salinity. However, incubation and early development of larvae of both Pacific and Atlantic herring have been found, under experimental conditions, to proceed normally in water of a salinity approaching that in which these processes occur naturally in the other "species" (McMynn and Hoar, 1953; Ford, 1929).

COLLECTIONS AND METHODS

Collections of Herring Larvae

For 5 consecutive years (1947 to 1951), herring larvae were sampled in the waters off the west coast of Vancouver Island. The sampling was carried out largely during the months of April and May in the vicinity of the spawning beaches, at places within the various bays and inlets, and off the outer coast beyond the mouths of the major sounds. Sampling was conducted at various depths and at all times of the day and night.

The surveys of 1947 and 1948 were of a preliminary nature. In those years the general distribution of herring larvae was determined and the most effective methods of collection established. In 1949, and particularly in 1950 and 1951, emphasis was placed on following the distribution and abundance of particular broods of larvae throughout the period of planktonic existence.

In all, 3973 samples of herring larvae were collected (Appendix 3). Of these, over two-thirds (2727) were taken on the lower west coast of Vancouver Island. The latter samples form, in large part, the factual basis of this manuscript. For special purposes, certain samples from the upper west coast of Vancouver Island (from Nuchatlitz Inlet in 1947 and from Queen Cove in 1949) have been used.

Complete records of data pertaining to all samples are filed at the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.

METHODS OF SAMPLING

Commercial seine-boats (from 70 to 80 ft in length, or 21 to 25 m), provided the means of reaching the remote areas of the west coast of Vancouver Island. Although some sampling was carried out directly from the seine-boats, most of it was conducted from small boats (about 18 ft, or 5.5 m, long) equipped with inboard motors. At times, operations were carried out from temporary field stations on shore.

Larvae were collected by three methods: (1) towing nets horizontally through the water, (2) pumping water from the sea and straining it through nets, and (3) attracting larvae to a light and collecting them with dip-nets. Sampling with nets proved to be the most practical and effective method and accounted for over 95% of the samples.

SAMPLING BY NETS

Four types of nets were employed in the course of the investigation: (1) cotton and silk nets of conventional conical shape, (2) silk nets of the Hensen egg-net design (Hensen, 1887), (3) Clarke-Bumpus samplers (Clarke and Bumpus, 1940), and (4) specially-designed metal nets (Tester and Stevenson, 1948). The principal specifications of each type of net are compared in Appendix 4.

The metal nets were designed to be towed from the seine-boat travelling at full speed of about 9 knots (17 km/hr). Other types of nets had to be towed at slower speeds (between 1 and 4 knots); boats about 18 ft (5.5. m) long, equipped with inboard motors, were employed for this purpose. The metal nets were particularly useful for sampling larvae in exposed offshore waters where the use of small boats was extremely hazardous to the life of personnel. Because of mechanical defects in construction, which could not be easily remedied, the metal nets were used only in 1948.

Although sampling was carried out to a depth of 30 fathoms (55 m), most samples were taken in the upper 4 fathoms (7 m) where the greatest concentration of larvae was found. Determination of the depth at which nets were being hauled was accomplished by trigonometric calculations based on the angle of the towing cable (with the horizontal plane) and the length of cable let out. Some error was involved in this technique as a result of the curvature of the cable caused by pressure of water against the forward cable surface. However, direct measurement of the actual depth of the net, using a fine wire, indicated that the trigonometric calculations were accurate within 10% at depths of 4 fathoms.

Silk nets were forced below the surface of the water during tows by using weights, and metal nets and plankton samplers were submerged below the surface by means of adjustable diving vanes. Greater depth was attained by increasing the length of the towing cable.

No devices were used to close the mouth of the net while the net was being lowered to and raised from the depth of sampling, in order to avoid contamination of samples with larvae at lesser depths. In general, it was considered that such contamination was small. Furthermore, since much of the sampling was done at night and under difficult weather conditions, the use of intricate closing devices would have greatly restricted the amount of sampling.

Sampling by pumping

The pump method of sampling (Tester and Stevenson, 1948) had two advantages over most other methods: (1) sampling could be carried out directly from the seine-boat in rough waters, and (2) the amount of water strained could be calculated exactly. It had, however, two serious disadvantages which limited its usefulness: (1) the amount of water strained per unit time was relatively small—about 1/15 that strained by the smallest silk net that was used, and (2) the larvae were usually badly damaged by the pump impellors.

Sampling by attracting larvae to lights

This method of sampling consisted of suspending a 100-watt bulb over the side of the seine-boat while at anchor and collecting larvae attracted to the light. No larvae less than 20 mm in length were taken by this method. The method failed to permit capture of larvae when even a relatively slight tidal current was flowing, presumably indicating that the power of locomotion of larvae was less than the movement of the water.

Field and Laboratory Treatment of Samples

The following data were taken for each sample of herring larvae:

a. Sample number
b. Place of sampling
c. Date
d. Time of day
e. Duration of sampling
f. Method of sampling
g. Length of cable released (in the case of sampling by nets)
h. Angle of towing cable (in the case of sampling by nets)
i. Calculated depth of sampling
j. Weather conditions
k. Remarks

The separation of the herring larvae from other organisms was carried out in the field whenever possible. No other clupeoid larvae were ever present in the samples. Young sand lance (***Ammodytes tobianus personatus*** Girard) and various species of larval flatfish were frequently taken. The most common invertebrates were coelenterates (several species of jellyfishes), ctenophores (mostly *Pleurobrachia* spp.), chaetognaths (*Sagitta* sp.), annelids (polychaetes), and crustaceans (cirriped larvae, amphipods, isopods, euphausiids, and decapod larvae).

In the laboratory, the separation of herring larvae from other organisms was completed, the larvae were counted and some or all were measured.

ESTIMATING THE NUMBER OF LARVAE IN SAMPLES

Counting the larvae posed no problem when they were not too numerous. However, in many samples several thousand were collected (up to 30,000), so a fraction of the sample (usually 1/6) was counted and the total number calculated from it. Extremely large samples were divided into several sub-samples (Appendix 5).

Statistical tests were used to assess the accuracy of this method for estimating the numbers of larvae in samples. In one experiment a sample was counted twice by the same person; the difference was not statistically significant ($F = 3.80$; $F_{.05} = 3.96$). In another experiment, the counts obtained by three persons working on the same sample were compared and showed no statistical differences: the variance between counts of samplers was considerably less than the variance for individual samples (error component). Differences between calculated numbers of larvae in a sample (determined by sub-sampling) and the actual counts (determined by counting all larvae in the samples) varied from 1.1 to 8.4%. Such differences are not great enough to lead to erroneous interpretations concerning the distribution of larvae in the sea. The results of these experiments are shown and discussed in Appendix 5.

MEASURING THE LENGTH OF LARVAE

Length measurements were made on 100 larvae from samples containing that many or more larvae, whereas in samples of fewer than 100 larvae all were measured. The larvae were measured from the tip of the snout to the end of the vertebral column. In the 1947 and 1948 collections, the length was determined to the nearest fifth of a millimeter, but, after 1948, measurements were made to the nearest half millimeter. All measurements were made on specimens preserved in a weak formalin solution (about 5%). The shrinking caused by the formalin amounted to about 2%.

The measuring apparatus consisted simply of two glass slides (3×2 inches; 76×51 mm) which were fastened together so that one slide partly overlaid the other. One of the edges of the upper slide crossed the centre line of the lower slide, forming a ridge along which larvae were placed for measuring. Along this ridge, a millimeter scale was suitably placed. Since the larvae were moist when measured, capillary action held the larvae tightly along the ridge, keeping them from curling. A hand lens was used to determine the precise location of the end points of the larva.

Two experiments were carried out in each of which five persons measured the lengths of the larvae in the same sample. One sample contained larger larvae than the other. Results of the experiments showed that the length frequency obtained by each worker was not statistically different from the averaged length frequency distribution of the five workers (Appendix 6). The mean length obtained by any worker varied only slightly from the mean length derived from the measurements of all workers—not exceeding 1.4% in the experiment with small larvae and not exceeding 0.5% in that with larger larvae.

Standardization of Numbers of Larvae in Samples

Differences between samples in numbers of larvae caught did not necessarily represent differences in concentration of larvae. In the first place, several sampling methods were employed which differed greatly in the amount of water strained during a haul. Secondly, it was not always possible to tow the nets for the standard length of time (10 minutes). Thirdly, the speed at which nets were towed varied considerably, according to the mechanical condition of the engine of the small towing boat, and the nature of the winds and tidal currents.

A method was developed to place the data on a reasonably quantitative basis. The numbers of larvae in each sample were adjusted, insofar as possible, to give the number of larvae that would have been taken if 10,000 Imperial gallons (45,500 litres) of water had been strained. The general formula adopted for this purpose was:

$$\frac{10{,}000}{t\,g} \times n$$

n being the actual number of larvae obtained in the sample, t the duration of sampling in minutes, and g the number of gallons of water strained per minute. Since n and t were known for each sample, the value of g referred to as the "straining capacity", had to be determined for each type of sampling gear. The methods used to determine the straining capacity of each type of sampling gear are discussed in Appendix 7.

DEVELOPMENT AND GROWTH OF HERRING LARVAE

At the time of hatching, herring larvae were found to be 4 to 8 mm long with an average about 6 mm (standard length: snout to end of vertebral column). Fujita and Kokubo (1927) and Ambroz (1931) found that herring of the western Pacific hatched at 8 mm but their measurements were based on total body length. Ehrenbaum (1905–09) reported that hatching of Atlantic herring occurred at standard lengths of 5.3 to 7 mm.

The yolk sac generally disappeared by the time the larvae reached 9 mm, but it was found lacking on individuals as small as 6 mm and it was still present in many specimens of 10 mm. Altnöder (1929) and Jespersen (1928) gave 9 mm as the usual length at which the yolk sac disapeared in Atlantic herring larvae in European waters.

During the yolk sac stage, the larva (or "prolarva", following the nomenclature of Hubbs, 1943) is semi-transparent and non-pigmented except for the black eyes. After the disappearance of the yolk sac, a characteristic pigmentation becomes evident on the ventral surface of the "postlarva" (Hubbs, 1943). It consists of two rows of chromatophores which are widely separated along the anterior half of the body, but which lie close together from the middle of the body back to the anus. In addition, a small number of larger pigment spots is found posterior to the anus and on the isthmus.

The pectoral fins become evident before the disappearance of the yolk sac, but the pelvic fins do not appear until a length of 21 to 24 mm is reached. The dorsal and caudal fins can usually be seen at 12 mm, and the anal fin at about 20 mm. According to Ehrenbaum (1905–09), the fins appear on attainment of similar body lengths in herring larvae from European waters.

Metamorphosis from postlarva to juvenile was found to begin at about 26 mm and to be complete at about 35 mm. One of the most striking features of the commencement of metamorphosis is greatly increased weight. Two 26 mm larvae which had not started to metamorphose weighed 0.06 and 0.07 g, whereas a larva of the same length but which had begun metamorphosis was found to weigh almost three times as much (0.17 g). Ogilvie (1927) and Marshall *et al.* (1937) refer to the great increase in the amount of food eaten by herring larvae at the onset of metamorphosis.

Metamorphosis appears to occur at a larger size of larva in the North Sea than on the British Columbia coast. Heincke (1898) found that the transitional stage began at a length of 31 to 34 mm for larvae from spring spawning herring and 44 to 60 mm for larvae from autumn spawners. Jespersen (1928), working in Danish waters, reported that metamorphosis began at 36 to 38 mm. Schach (1939) obtained, in laboratory experiments on Atlantic herring larvae, a rate of development which closely resembled that of British Columbia herring larvae—complete metamorphosis at lengths of 30 to 40 mm.

Data are presented in a later section (see Fig. 17) which indicate that rate of growth of larvae hatched in early April is considerably less than that of larvae hatched in early May. In the former larvae the growth was approximately 0.3 mm per day, whereas in the latter it was about 0.8 mm per day.

These results would suggest that the greater growth of late-hatched larvae is associated with increased temperature of the water. Several workers on Atlantic herring larvae have shown the effect of temperature on rate of development and growth (Schnakenbeck, 1929; Kotthaus, 1939; Bowers, 1952; Jean, 1955). Pronounced differences have been found between the growth of larvae from fall-spawning and from spring-spawning herring. The slow growth of the former has been attributed to the low temperatures prevailing during the winter, and the small amount of food in the water at that period of the year.

VERTICAL DISTRIBUTION OF HERRING LARVAE

Early in the present investigation, considerable variations in concentration of larvae were noted at different depths and at different hours of the day and night. Because of these variations it was evident that a study of vertical distribution was necessary to determine where and when sampling of a particular brood should be carried out to reflect the general abundance. Such information appeared essential in order that the horizontal distribution, and the survival, of herring larvae could be followed throughout the period of larval life.

Knowledge of the vertical distribution, and particularly information on the depth and time of day that larvae were most densely concentrated, was also important for interpreting the effect of water currents on the horizontal displacement of larvae.

Variation in Concentration of Larvae with Depth

Herring larvae are usually most highly concentrated near the surface of the water, but changes in the depth distribution are apparent with increase in growth.

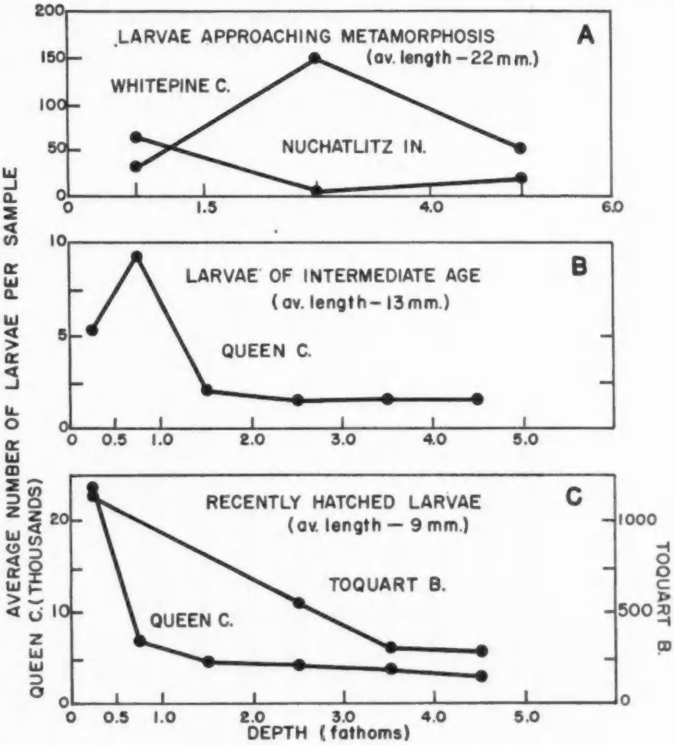

Fig. 4. Concentration of herring larvae at various depths according to larval development. Points are plotted in middle of depth zones.

In Toquart Bay in 1950, about 4 times as many newly-hatched larvae were taken in the 0–0.5 fathom depth zone as in the 4–5 fathom zone, and in Queen Cove almost 7 times as many (Fig. 4 and Appendix 8). The depth of both sampling areas was about 6 fathoms (11 m), but sampling could not be carried out deeper than 5 fathoms (9 m) for fear of snagging the net on the bottom. When the larvae increased in size to an average length of about 13 mm, the tendency to be concentrated in surface waters still remained, but it was less pronounced (Fig. 4 and Appendix 8). With further increase in size and the approach of metamorphosis, the pattern of depth distribution was less consistent (Fig. 4). Sometimes greatest abundance was still at the surface (e.g., in Nuchatlitz Inlet in 1947), whereas at other times fewer larvae were found in the surface zone than at greater depths (e.g., in Whitepine Cove in 1947).

The newly-hatched larvae and the larvae approaching metamorphosis showed no noticeable segregation according to size, with increasing depth. Larvae of intermediate age, however, were of significantly greater average length in samples taken below 1 fathom (1.8 m) than in samples above ($P<0.001$—Appendix 9). The length frequency distribution of larvae below and above this depth clearly showed the reason for the difference in average length (Fig. 5 and Appendix 9). A second hatching had recently occurred and gave a distinct bimodality to the length frequency distribution. The newly-hatched larvae were highly concentrated in the 0–1 fathom zone, resulting in a low average length of the larvae from samples taken at that depth.

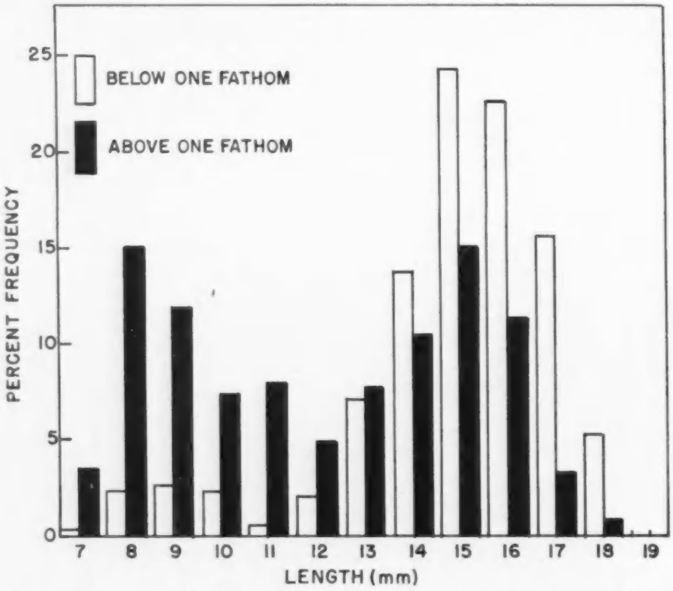

FIG. 5. Percentage length frequency of larvae from Queen Cove on April 21–25, 1949, above and below a depth of 1 fathom (1.8 m).

VARIATION IN CONCENTRATION OF LARVAE BETWEEN DAY AND NIGHT

The numbers of larvae at all depths varied with the time of day that sampling took place.

To study the vertical distribution of larvae during the day and night, two series of samples were taken every 3 hours over a 24-hour period. The first series was taken in Queen Cove on April 20–21, 1949, and the second series in Toquart Bay on April 8–9, 1950. The sampling was carried out at 2 depths, at 0–1 fathom (0–1.8 m) and at 2–4 fathoms (3.7–7.3 m). The average numbers of larvae in each 3-hour period are shown in Fig. 6 and 7 and in Appendix 10, together with the changes in average lengths of larvae over the 24-hour period of sampling. The data are summarized in Table I, by averaging all daylight samples together and all night samples together.

CONCENTRATION NEAR SURFACE AT NIGHT

As expected on the basis of the previous discussion on changes in numbers of larvae with depth, the samples taken in the surface zone during the 24-hour sampling series contained more larvae than samples taken in the deeper zone. About 25 times more larvae were taken at the surface than in the 2–4-fathom zone in Toquart Bay (Table I). This tendency was consistent throughout the hours of the day and night (Fig. 7).

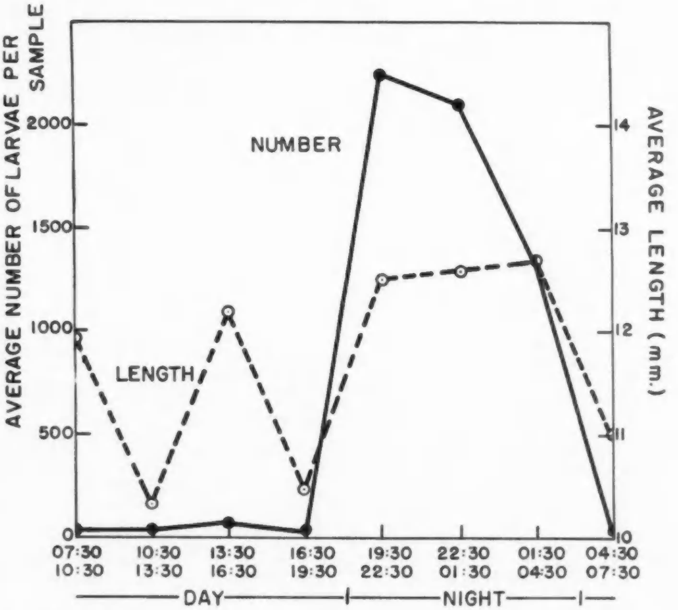

FIG. 6. Average number and average length of larvae in samples taken every three hours at a depth of 0–1 fathom (0–1.8 m) on April 20–21, 1949, in Queen Cove.

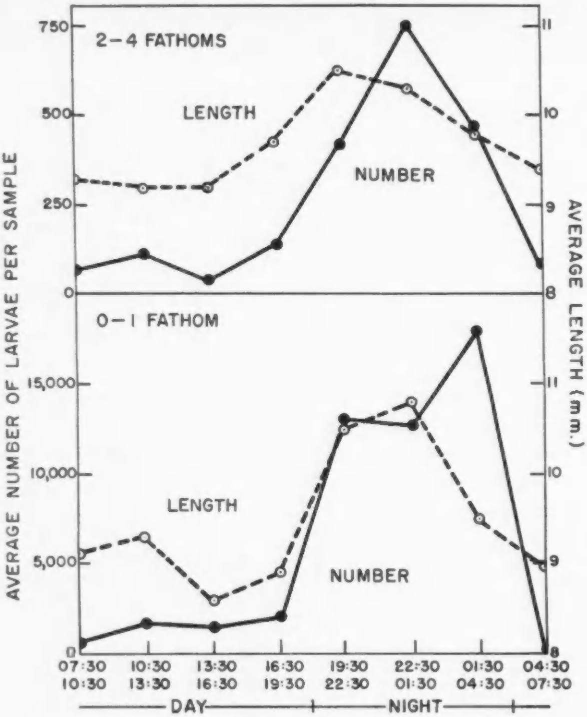

FIG. 7. Average number and average length of larvae in samples taken every three hours at depths of 0–1 and 2–4 fathoms (0–1.8 and 3.7–7.3 m) on April 8–9, 1950, in Toquart Bay.

TABLE I. Average numbers of larvae per sample in two localities according to day and night sampling and according to shallow and deep sampling. Number of samples is shown in parentheses. *Shallow* = 0–1 fathom, 0–1.8 m; *deep* = 2–4 fathoms, 3.7–7.3 m. Larvae from Queen Cove had a greater average length than those from Toquart Bay — 11.6 mm and 9.6 mm, respectively. (See also Appendix 10.)

Time	Queen Cove			Toquart Bay		
	Depth of sampling			Depth of sampling		
	Shallow	Deep	Both	Shallow	Deep	Both
Day	38 (13)	52 (4)	45	1,332 (13)	87 (13)	710
Night	1,890 (9)	793 (3)	1,341	14,533 (10)	544 (10)	7,538
Both	964	422	693	7,932	316	4,124

Samples taken during the night invariably contained more larvae than samples taken during the day, regardless of depth of sampling (Fig. 6 and 7, Table I). In Queen Cove, about 30 times more larvae were taken in night sampling than in daylight sampling.

The abrupt increase in the numbers of larvae with the coming of night was clearly shown in sampling in the surface zone. Between 16:30 and 19:30 hours in Queen Cove, an average of 24 larvae was taken per haul; at 20:00 hours (dusk), 370 larvae per sample were taken; and at 22:00 hours, 4150 larvae were obtained per sample.

The data from the two series of samples taken over a 24-hour period failed to suggest that a uniform pattern of changes in concentration of larvae occurred either through the hours of the night or through the hours of the day.

Larger larvae taken at night

Larvae derived from sampling at night were generally larger than those taken during the day (Fig. 6 and 7, and Appendix 10). The average length of larvae taken in Toquart Bay during the daytime was 8.93 mm, while at night it was 10.05 mm. This difference was of high statistical significance ($P < 0.001$—Fig. 8 and Appendix 11). The average length of larvae in Queen Cove was 11.1 mm during the day and 12.3 mm at night.

No pronounced difference could be detected in the average length of larvae with increase in depth, such as was noted in the detailed data on depth distribution. The samples analyzed in the previous discussion contained two broods of larvae of different age, and a comparison was thereby possible between larvae of two distinct length-groups. In the present data, a single brood was involved and the range of size was relatively small. Moreover, only 2 depth zones are compared here as against 6 in the previous data; thus, differences in average length of larvae with change in depth may have been obscured by the restricted depths at which sampling was undertaken.

Difference in vertical distribution between two localities of sampling

The data summarized in Table I suggested that differences existed between the vertical distribution of larvae in Queen Cove and in Toquart Bay. The preponderance of larvae in night hauls over day hauls was greater in Queen Cove than in Toquart Bay (30 times as compared to 11 times). On the other hand, the preponderance of larvae taken at the surface over those taken at 2–4 fathoms was less in Queen Cove than in Toquart Bay (about 2 times as compared to 25 times).

Another difference was noted between the distribution of larvae in Queen Cove and in Toquart Bay. In Queen Cove, the data suggested (Fig. 6 and 7, and Appendix 10) that the greatest number of larvae found during the night (at the surface) was before midnight (19:30 to 22:30 hours), but in Toquart Bay the largest concentrations were found after midnight (01:30 to 04:30).

Two possible causes for such apparent difference in the distribution pattern of larvae were considered: (1) differences in the amount of illumination on the

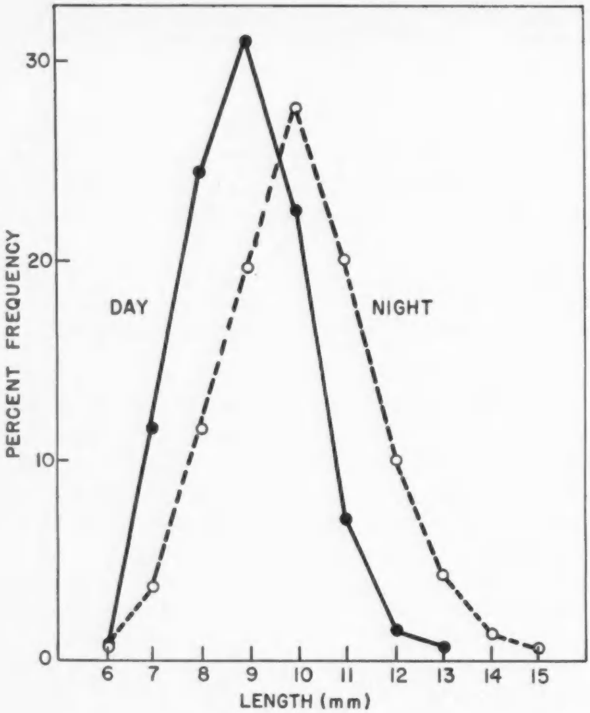

FIG. 8. Percentage length frequency of larvae from Toquart Bay during the day and during the night on April 8–9, 1950.

water during the night sampling in the two areas and (2) differences in the development and average size of the larvae in the two areas.

Marked decreases in the abundance of larvae were observed in night sampling at two localities in 1950 before and after the rising of a bright moon (Table II). However, during the two nights of sampling in Toquart Bay and Queen Cove, no difference in illumination was perceived either between nights or during either night. Both nights were equally dark with heavy cloud cover and no moon.

A difference was noted, however, in the average length of larvae in the two areas. In Queen Cove, the larvae were larger than those in Toquart Bay—average length of 11.6 mm and 9.6 mm, respectively.

The difference in average length of the larvae in the sampling areas implies that a change in behaviour of larvae occurs when the larvae reach a length of about 10 or 11 mm. Presumably at this stage of development, they tend (1) to become relatively more numerous in the deeper water than they were when younger, (2) to become relatively more numerous in night sampling (at all depths) than in day sampling, and (3) to be more concentrated in the surface layer before midnight than after midnight.

TABLE II. Average numbers of larvae in samples taken at night under dark cloudy conditions and under conditions of bright moonlight.

Place and date	Time	Depth of sampling				Brightness
		0–1 fa, 0–1.8 m		2–4 fa, 3.7–7.3 m		
		No. of samples	No. of larvae	No. of samples	No. of larvae	
Stopper Islands April 7, 1950	01:00	3	34,880	3	647	Cloudy, moon obscured
	02:00	2	15,870	2	604	Clear, full moon
Nettle Island April 26, 1950	21:00	3	945	6	17	Cloudy, before moon rose
	22:00	4	165	2	50	Clear, bright moon

Results of sampling at Whitepine Cove on May 18–20, 1947, suggested that the tendency to be more densely concentrated before midnight than after midnight remains at least until just prior to metamorphosis. The Whitepine Cove larvae (average length, 22.4 mm) showed highest numbers in samples taken between 22:00 to 23:00-hours (Table III).

TABLE III. Average numbers of larvae taken in samples from Whitepine Cove on May 18–20, 1947, during each hour of the night.

Time	No. of samples	Av. no. of larvae	Av. length of larvae
			mm
22:00–23:00	5	299.2	23.1
23:00–24:00	5	211.0	22.2
24:00–01:00	3	42.3	22.9
01:00–02:00	4	150.5	22.8
02:00–03:30	5	13.4[a]	21.0

[a] The decrease in numbers of larvae in this period was undoubtedly a result of the coming of dawn (a noticeable brightening of the sky occurred about 02:45 hours).

EFFECT OF LIGHT INTENSITY ON VERTICAL DISTRIBUTION OF LARVAE

The foregoing results suggest that the distribution of herring larvae according to depth and time of day is governed by the reaction of larvae to light and by changes in the nature of that reaction as the larvae develop.

Newly-hatched larvae (up to about 8 mm in length) were found heavily concentrated in surface waters. The tendency for newly-hatched larvae to stay at the surface was as strong during the day as during the night. For the period, March 26 to April 5, 1949, the average number[4] of larvae per sample in the surface zone at Queen Cove was 22,600 in daylight sampling and 21,800 in night sampling. Schach (1939) and Bückmann *et al.* (1953) suggest the explanation of these observations by showing experimentally that newly-hatched larvae have a strong attraction to light of widely different intensity. The strength of this attraction is indicated by the fact that herring larvae are of greatest specific gravity during the yolk sac stage, and that newly-hatched larvae would therefore have a greater tendency to sink to the bottom than older larvae (Ford, 1929).

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[4] Daylight and night sampling in Queen Cove during this period are combined in Appendix 8, showing an average of 22,480 larvae per sample in the surface zone.

The large concentrations of larvae during the yolk sac stage, noted in both day and night sampling in shallow water near the spawning grounds, decreased considerably by the time that the larvae lost the yolk sac. At the same time a pronounced tendency developed for greater numbers of larvae to be taken in night sampling than in day sampling, and for larger numbers to be taken in the surface zone than in deeper zones. This was shown for larvae averaging 9.6 mm in length in Toquart Bay (Fig. 7, Table I), where 11 times more larvae were taken in surface hauls at night than during the day and 6 times more were taken in deeper hauls at night than during the day. Slightly larger and older larvae from Queen Cove, averaging 11.6 mm in length, showed an even more striking difference in numbers taken in day and night sampling (Fig. 6, Table I), with night hauls producing 30 times the number of larvae in daytime hauls in the surface zone and 16 times the number of larvae in the deeper zone. Also, the data suggested that although much greater numbers of larvae were found in the surface zone than in deeper zones immediately after the loss of the yolk sac (larvae of about 9 to 10 mm in length), this difference in numbers of larvae between the surface and deeper zones decreased as the larvae grew to 11 to 13 mm in length (Fig. 4, Table I).

The experimental results of the European investigators Schach (1939) and Bückmann *et al.* (1953) led to the conclusion that Atlantic herring larvae are strongly attracted to light during the entire larval period. The results summarized above do not support this view, at least in so far as for Pacific herring larvae are concerned. That newly-hatched larvae are strongly attracted to light of all intensities cannot be disputed. However, after the absorption of the yolk sac, the present data indicate that the reaction to light becomes more complex. Evidence suggests that the influence of light varies with its intensity. Johnson (1937) has emphasized that the positive and negative phototropism exhibited by adult Atlantic herring can only be interpreted through analysis of reaction to light of different intensity.

It is suggested that immediately after the absorption of the yolk sac, the larvae undergo a change in their reaction to light whereby they are repelled by strong light but they remain attracted by light of weak intensity. This would explain the striking decrease in the number of larvae taken in day sampling after the absorption of the yolk sac (repelled by strong light), and the large numbers that continued to be taken in night sampling, especially near the surface (attracted by the weak light of the night sky). On the basis of this explanation it would appear that the intensity of bright moonlight was sufficiently great (like daylight) to have a repelling effect on larvae in the surface zone (Table II).

Also, it might be considered that larvae shortly after the absorption of the yolk sac were more attracted to weak light than slightly older larvae (Table I).

On the basis that daylight causes the larvae to avoid the surface waters it would be expected that large numbers of larvae would be found in deeper water during the daytime. However, sampling during the day did not reveal concentrations at any depth comparable to those found at the surface at night. This fact led to the conclusion that the larvae were not heavily concentrated during the daytime but were distributed over a wide range of depth. No completely satisfactory explanation of this can be given in terms of the reaction of larvae to light but it is considered possible that the water in areas in which larvae were generally found was too shallow (rarely exceeding 10 fathoms) to permit the larvae from reaching a depth where the preferred intensity of light could be attained. Jean (1955), in studying Atlantic herring larvae near Grand River, Quebec, similarly found no heavy concentrations at any depth down to about 12 fathoms in daytime sampling. European investigators, Johansen (1925) and Jensen (1950), were however able to locate concentrations of Atlantic herring larvae at depths of about 15 fathoms during the daytime that were comparable to the surface concentration at night. These observations suggest the possibility that during the day larvae tend to concentrate at a depth above which the light is strong enough to repel the larvae and below which it is too weak in intensity to attract them, and that in the case of herring larvae in British Columbia waters the shallowness of the brood areas prevents this concentration from taking place.

Another factor contributing to the smaller number of larvae at all depths in daytime sampling was probably the greater ability of the larvae to escape sampling gear during the day than during the night. This evasion of the nets appeared to increase with increasing age of the larvae, until after attaining a length of about 16 mm practically no larvae were taken by day sampling. Since large larvae tended to stay deeper in the water than smaller larvae (Fig. 5), evasion of the sampling gear would be expected to be greater in deep water than in shallow. This might tend to account for the fact that surface samples usually contained more larvae than deep samples during the day, even though it is probable that greater numbers of larvae were present in deep layers than near the surface in the daytime.

A third major change in reaction to light was noted beginning when the larvae reached about 18 mm in length and continuing at least until metamorphosis was reached. During this period and particularly just before metamorphosis they showed a strong attraction to bright light, as indicated by the fact that they could be collected using an electric light suspended over or immersed in the waters of the brood areas. This behaviour was observed by McHugh (1940) throughout the period of metamorphosis. The attraction of adult herring to bright lights at night is well established.

Because of the somewhat complicated pattern of vertical distribution, it was not particularly easy to decide at what depth and what time of day sampling would best indicate general abundance. However, in view of the pronounced tendency for the larvae to concentrate at the surface during the night, it appeared that sampling under those conditions should be moderately representative of the actual abundance of larvae. Sampling was, therefore, conducted mostly during the night in the 0–1 fathom layer (0–1.8 m). The data presented in the following sections to illustrate the horizontal distribution of herring larvae are based entirely upon this system of sampling.

HORIZONTAL DISTRIBUTION OF HERRING LARVAE

The northern part of Barkley Sound was chosen for investigation of the horizontal distribution of herring larvae. The main reason for selecting this area was the fact that extensive spawnings occur there each year. About 75%, on the average, of the herring of the lower west coast of Vancouver Island spawn in this area.

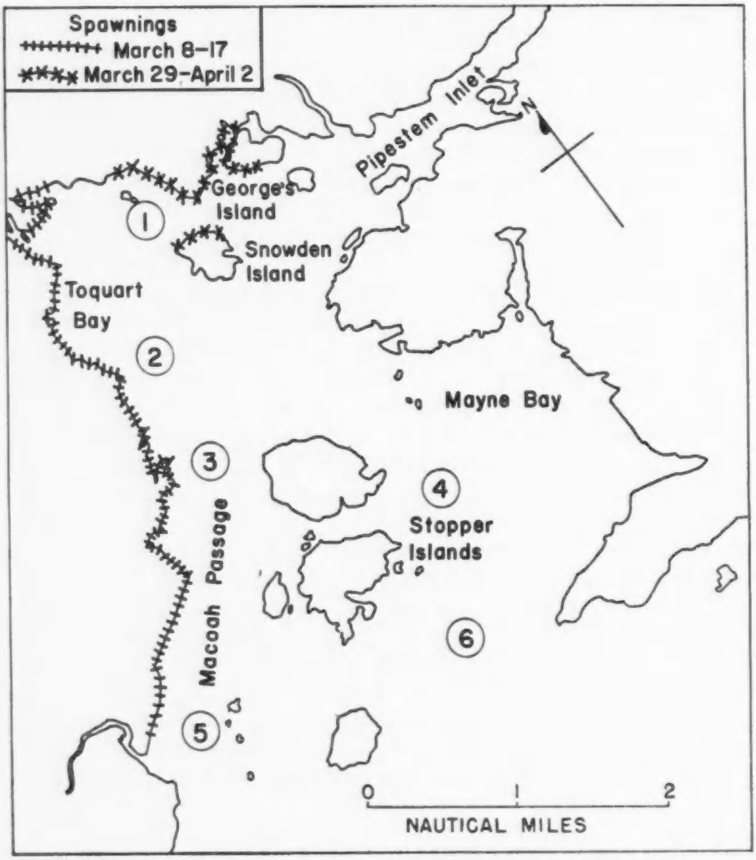

Spawnings
March 8–17
March 29–April 2
Pipestem Inlet
N
George's Island
1
Snowden Island
Toquart Bay
2
Mayne Bay
3
4
Stopper Islands
Macoah Passage
6
5
0
1
2
NAUTICAL MILES

FIG. 9. Map of Toquart Bay and vicinity showing the location of the spawnings that occurred in 1951 and the location of the larval sampling stations in that year.

An intensive program of larval sampling was carried out in the spring of 1950 to study the distribution of larvae over the entire area. In the spring of 1951, a special study was conducted on the distribution of larvae in one part of the area (Toquart Bay and vicinity), where particularly heavy spawnings usually occur. It appears desirable to discuss the results of the localized study of 1951 before dealing with the results of the more comprehensive 1950 survey.

Distribution of Larvae in Toquart Bay in 1951

Time and location of spawnings

The first spawning in the northern part of Barkley Sound in 1951 occurred on February 11 along Macoah Passage. This spawning was hatched before sampling for larval herring began.

The main spawning began in Toquart Bay on March 8 and continued until March 17. During this time, spawn was deposited along practically the entire shore of Toquart Bay and southwesterly along the Vancouver Island shore of Macoah Passage to the Maggie River (Stevenson *et al.*, 1951). The most intensive spawning occurred in Toquart Bay on the broad delta of the Toquart River and to the west (Fig. 9), where it was estimated that 80% or more of the spawning occurred.

No other spawning was recorded in this area until March 29 when a small spawning, involving not more than one-tenth the number of spawners in the March 8–17 spawning, took place in Toquart Bay east of the Toquart River and around George's Island. On April 1–2, a similarly small spawning occurred along the northeast shore of Snowden Island.

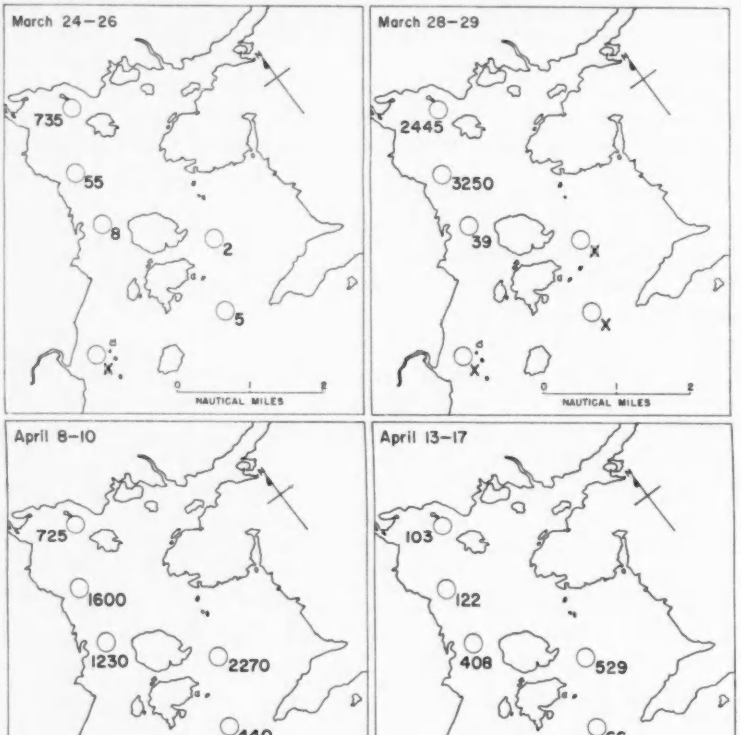
Abundance of larvae at different periods during the survey

The average numbers of larvae per tow are shown at 6 selected sampling stations for 11 periods during the course of the survey in Fig. 10. Length frequency data of the larvae sampled are given in Appendix 12.

The sampling began on March 24, about the time the first eggs (those spawned on March 8) were beginning to hatch. Sampling continued until May 21, but after May 17 no larvae were captured.

Early period of hatching. During the first period of sampling (March 24–26), moderately large numbers of larvae were taken at the head of Toquart Bay (Station 1), but very few were found outside the Bay (Stations 3, 4, and 5). The sparsity of larvae outside the Bay strongly suggested that hatching from the large spawning of March 8–17 had only recently begun, while the concentration of larvae inside the Bay was indicative of the fact that the earliest spawning (March 8) had occurred in that area.

Examination of the length frequencies of the larvae in six samples taken in the March 24–26 period indicated that two distinct size (and age) groups of larvae were present in the Bay. Three of the samples contained larvae which averaged 7.2 or 7.3 mm in length, whereas the other three were composed of larvae averaging 8.5 to 8.9 mm (Appendix 13). The difference between the average lengths of the two groups was statistically significant ($P<0.001$).


March 24–26
735
55
8
2
5
X
0 1 2
NAUTICAL MILES
March 28–29
2445
3250
39
X
X
X
0 1 2
NAUTICAL MILES
April 8–10
725
1600
1230
2270
440
830
0 1 2
NAUTICAL MILES
April 13–17
103
122
408
529
66
237
0 1 2
NAUTICAL MILES
April 29–30
9
7
19
37
4
18
0 1 2
NAUTICAL MILES
May 3–7
5
7
26
37
6
8
0 1 2
NAUTICAL MILES

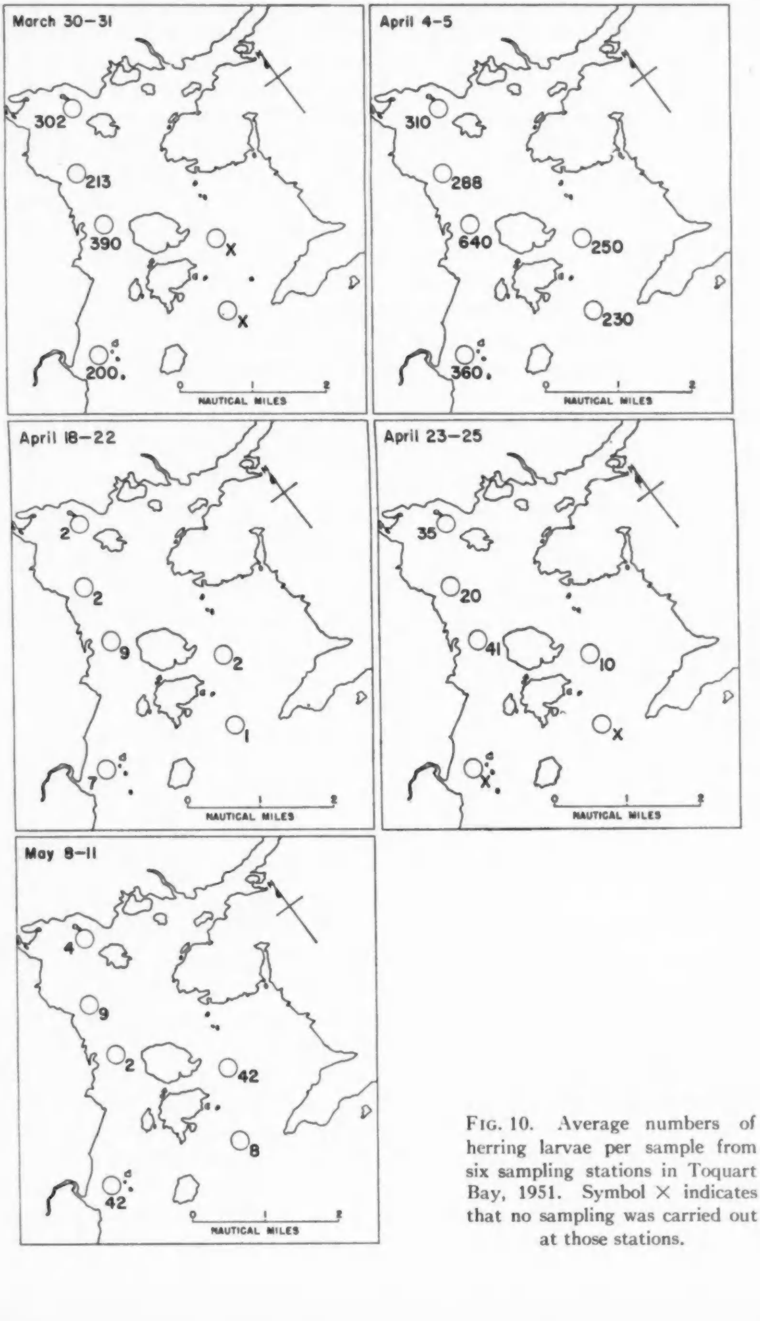

March 30–31
302
213
390
X
X
200
0
1
2
NAUTICAL MILES
April 4–5
310
288
640
250
230
360
0
1
2
NAUTICAL MILES
April 18–22
2
2
9
2
1
7
0
1
2
NAUTICAL MILES
April 23–25
35
20
41
10
X
X
0
1
2
NAUTICAL MILES
May 8–11
4
9
2
42
8
42
0
1
2
NAUTICAL MILES

FIG. 10. Average numbers of herring larvae per sample from six sampling stations in Toquart Bay, 1951. Symbol × indicates that no sampling was carried out at those stations.

Hatching continued throughout this 3-day period, a result of the fact that spawning had extended over several days. The existence of these distinct groups of larvae in the Bay suggested that transfer of newly-hatched larvae from the immediate vicinity of the spawning grounds to the centre of the Bay was intermittent. It will be suggested, in a later section, that this segregation of newly-hatched larvae (noted only in the early period of hatching) was a result of the action of the tide.

A temporary holding of newly-hatched larvae on the spawning beaches by tidal currents might explain the scarcity of very small larvae in the samples. While observations have shown that 6 mm is the average length on hatching, most larvae are 7 or 8 mm long when they are first taken in samples. Because of the shallow water over most of the spawning grounds, sampling operations cannot usually be carried out there. Thus, by the time the larvae are available to the sampling gear, they would have increased from their initial hatching size. This explanation postulates an extremely rapid growth in the short time frequently intervening between hatching and sampling. Jones (1948) gives evidence that growth during the period of the absorption of the yolk sac is greater than at any other period of the larval stage.

PERIOD OF GREATEST ABUNDANCE IN TOQUART BAY. On March 28–29, the abundance of herring at Station 1 increased greatly, and large numbers of larvae had apparently moved towards the mouth of the Bay (Station 2). No appreciable dispersal of larvae had occurred outside the Bay (Station 3).

Hatching was still going on in Toquart Bay, but on a reduced scale. Larvae of 7 mm were less abundant than larvae of 8 and 9 mm.

From the beginning of the sampling, a small number of larvae of 11 to 15 mm was taken in Toquart Bay. These were presumably from the February spawning in Macoah Passage. The relatively large proportion of these older larvae at Station 3 on March 28–29, as well as the small total numbers of larvae at that Station, emphasized the very limited extent of movement of the recently-hatched larvae out of the Bay.

MOVEMENT OF LARVAE OUTSIDE TOQUART BAY. On March 30–31, approximately one week after hatching started, the larvae had moved from the head of Toquart Bay (Station 1) to the mouth of the Maggie River (Station 5)—a distance of 3.7 nautical miles (6.9 km). There is little doubt that the 10 mm larvae from Station 5 were derived from the first hatching in Toquart Bay; these larvae comprised about $\frac{1}{4}$ of the catches from this Station. The 8 mm larvae, which were equally numerous, were either from later hatching in Toquart Bay or from hatching of spawn in Macoah Passage.

With the appearance of larvae outside the Bay, the numbers of larvae inside showed a noticeable decrease. In fact, at the head of the Bay, the samples contained practically no larvae from the early hatching, but were composed mainly of newly-hatched larvae of 7 and 8 mm.

Five days later (April 4–5), the abundance over the entire area was little changed. Hatching had been going on, but probably mainly in Macoah Passage. The earliest-hatched larvae had reached a length of about 11 or 12 mm.

SECOND MAJOR PERIOD OF HATCHING. By April 8–10, the pronounced increase in larval abundance at stations around the Stopper Islands suggested that the main hatching of spawn in Macoah Passage had taken place, probably on about April 5 or 6. An increase occurred in larval abundance at the head of Toquart Bay, but it was relatively small, suggesting that hatching in that area was nearly complete.

The small spawning east of the Toquart River to George's Island was probably hatching about this time, but the numbers of larvae were undoubtedly too small to be distinguished in the sampling.

GENERAL DECREASE IN LARVAL ABUNDANCE. The sampling period of April 13–17 showed a decrease in numbers of larvae at all stations, and a further, more pronounced, decrease occurred on April 18–22. A small increase in abundance took place near the end of April as a result of hatching of larvae from a small spawning that had not been previously recorded. This brood could be readily distinguished from earlier broods on the basis of length frequency (Appendix 12).

The numbers of larvae taken after May 11 were very small. In 55 samples taken from May 12–21, a total of only 22 larvae was taken.

DISTRIBUTION OF LARVAE IN NORTHERN BARKLEY SOUND IN 1950

TIME AND LOCATION OF SPAWNINGS

The main spawning in the northern part of Barkley Sound in 1950 occurred at about the same time as in 1951—March 5–13 as compared to March 8–17. The amount of spawn deposited in the main spawning was similar in both years. But whereas an estimated 10 times as many herring spawned in Toquart Bay as in Macoah Passage in 1951, approximately the same number of herring spawned in each area in 1950 (Stevenson and Lanigan, 1950).

The amount of spawning that took place in late January and early February in 1950 was similar to other years. This spawn had hatched before the beginning of the larval survey.

Two late spawnings occurred, a small spawning in Mayne Bay and near the Maggie River on March 29, and a somewhat larger one on the shore of Nettle Island on April 3.

The spawnings are indicated in Fig. 11.

ABUNDANCE OF LARVAE AT DIFFERENT PERIODS DURING THE SURVEY

The average numbers of larvae per tow are shown during 6 periods of sampling in Fig. 12. Sampling was carried out in 7 sectors of the northern part of Barkley Sound (referred to as A–G), and 6 regular sampling stations were selected in each sector (Fig. 11). Four additional sampling stations in Sector E and 2 in Sector F were used in the April 21–25 period. Length frequency data for samples taken at each station are given in Appendix 14.

Sampling began on April 1, and continued until May 30.

EARLY ABUNDANCE CONFINED TO TOQUART BAY AND VICINITY. In the April 4–8 period, high abundance of larvae was found in Toquart Bay, Macoah Passage-Stopper Islands, and Mayne Bay (Sectors A, B and C). Length

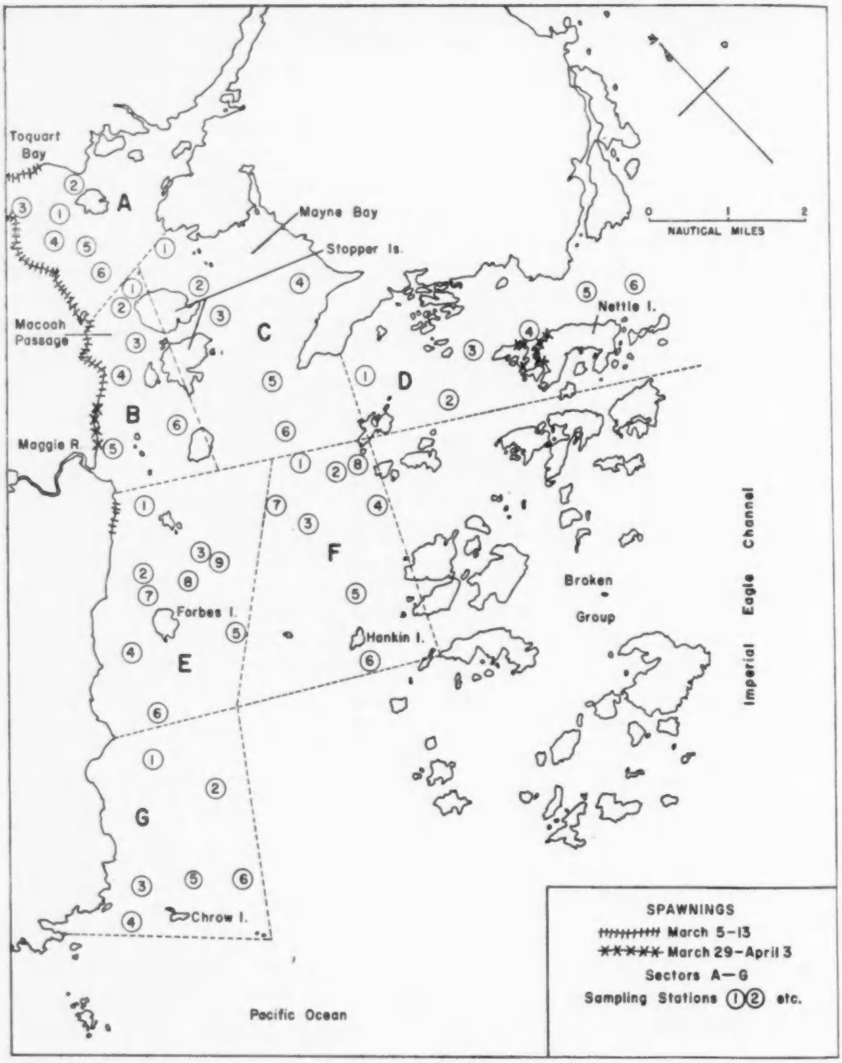

Toquart Bay
A
Mayne Bay
Stopper Is.
Macoah Passage
B
C
D
Nettle I.
Maggie R.
E
F
G
Forbes I.
Hankin I.
Chrow I.
Broken Group
Imperial Eagle Channel
Pacific Ocean
0 1 2
NAUTICAL MILES
SPAWNINGS
March 5–13
March 29–April 3
Sectors A—G
Sampling Stations ①② etc.

FIG. 11. Map of the northern part of Barkley Sound showing the location of the spawnings that occurred in 1950, the seven sectors into which the area was divided, and the sampling stations in each sector.

frequency data suggested that the hatching of the main spawning of March 5–13 had been going on for a few days prior to the beginning of sampling on April 1. The number of larvae hatched before April 1 was apparently small, but a marked increase was noted after April 1, reaching a peak both in the Toquart Bay and in the Macoah Passage-Stopper Islands Sectors on April 7 and 8.

No hatching occurred within Mayne Bay (Sector C) in this period. The large concentration of larvae there was evidently the result of movement from the Toquart Bay and Macoah Passage-Stopper Islands Sectors (A and B).

Sampling in the Forbes Island Sector (Sector E) in this period showed low abundance of larvae. Hatching was not going on within this Sector and no appreciable movement to this Sector of larvae hatched elsewhere had occurred.

MOVEMENT OF LARVAE TOWARDS THE MOUTH OF BARKLEY SOUND. By April 13–15, two significant changes had occurred in the distribution of larvae in the northern part of Barkley Sound. Sampling in the vicinity of the spawning grounds (Sectors A and B) gave sharply reduced numbers of larvae, while a considerable increase in larval abundance was noted in the Forbes Island Sector (E). High abundance was also noted in adjoining portions of the Mayne Bay and Hankin Island Sectors (C and F).

Since there was no evidence that any appreciable hatching had occurred outside of the Toquart Bay and Macoah Passage-Stopper Islands Sectors, the increased abundance of larvae in the aforementioned Sectors must have occurred through seaward movement of larvae.

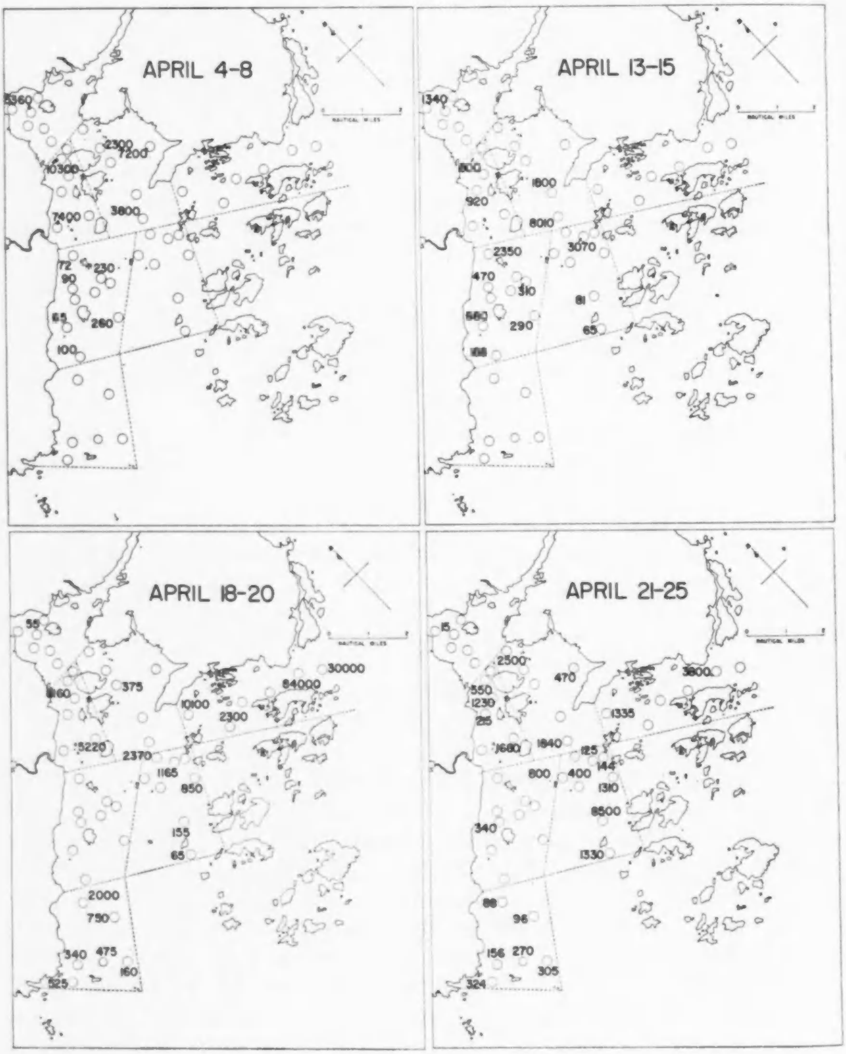
In contrast, abundance was low in the outer portion of the Hankin Island Sector. There are two possible explanations, which will be discussed later: (1) larvae moving seaward had not time to reach this area, and (2) water movements were such as to prevent larvae hatched in the Toquart Bay-Macoah Passage Sectors from reaching this area.

NEW HATCHING AND FURTHER SEAWARD MOVEMENT. In the period of April 18–20, hatching recommenced in the Macoah Passage-Stopper Islands Sector (B), and began in the Nettle Island Sector (D). Hatching apparently reached a peak in both these areas on April 18 or 19.

At the same time, larvae from the early period of extensive hatching (in the Toquart Bay and Macoah Passage-Stopper Islands Sectors on April 7 and 8) had reached the mouth of Barkley Sound in the Chrow Island Sector (G). But, as noted in the previous period (April 13–15), larvae had not moved in appreciable numbers to the outer part of the Hankin Island Sector (F). (The average number of larvae per sample in the outer part of the Hankin Island Sector during the combined periods of April 13–15 and April 18–20 was significantly less than the average number of larvae per sample in the Forbes Island and Chrow Island Sectors during the same periods—Appendix 15.)

MOVEMENT OF LARVAE FROM THE NETTLE ISLAND SECTOR. The most striking feature of larval distribution on April 21–25 was high concentration of larvae in the outer portion of the Hankin Island Sector (F), the area that previously was characterized by low abundance. No spawnings had taken place in this Sector, and on the basis of the age of larvae found in this Sector, as indicated by length frequency data, the larvae appeared to have come from the Nettle Island Sector (D) hatching which reached a peak on April 18 and 19.

These facts strongly indicated that larvae from these two spawning areas—Toquart Bay-Macoah Passage (Sectors A and B) and Nettle Island (Sector D) moved seaward by different routes: (1) larvae from Toquart Bay-Macoah Passage spawnings moving along the northwest shore of Barkley Sound through the Forbes Island and Chrow Island Sectors (E and G) and (2) larvae from the Nettle Island spawning moving to the Hankin Island Sector (F), and especially to the outer portion of this Sector. The influence of water movements in Barkley Sound (Fig. 14) on the seaward movement of larvae will be discussed in a later section.


APRIL 4-8
5360
2300
7200
10300
7400
3800
72
230
90
65
260
100
NAUTICAL MILES
APRIL 13-15
1340
800
1600
920
8010
2350
3070
470
310
81
560
290
65
166
NAUTICAL MILES
APRIL 18-20
55
375
30000
8160
84000
10100
2300
5220
2370
1165
850
155
65
2000
750
340
475
160
525
NAUTICAL MILES
APRIL 21-25
15
2500
470
3800
550
1230
215
1335
1680
1840
125
144
800
400
1310
8500
340
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96
156
270
305
324
NAUTICAL MILES

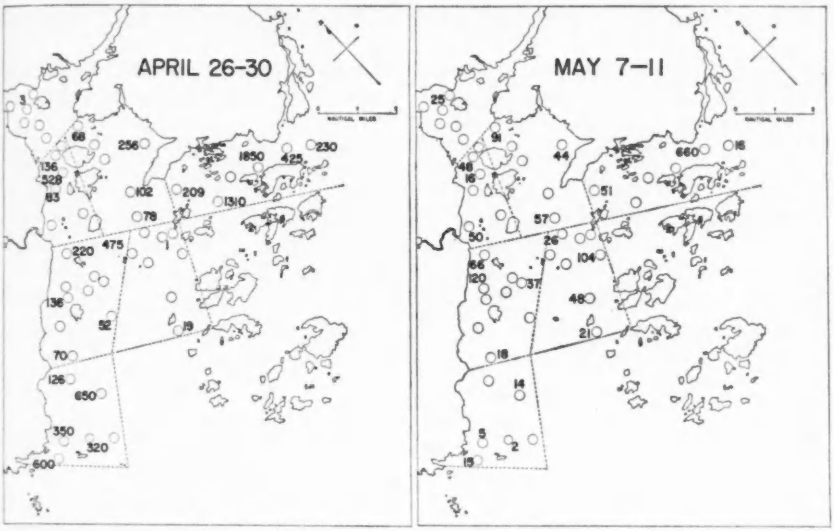

FIG. 12. Average numbers of herring larvae per sample at various stations in the northern part of Barkley Sound in six periods during the spring of 1950. (The average numbers of larvae, indicated in the figure, frequently represent a combination of data from two or more neighbouring stations which showed similar larval concentration.)

A second surge of hatching occurred in the Nettle Island Sector during this period.

DISTRIBUTION OF LARVAE AFTER COMPLETION OF HATCHING. After April 26, large-scale hatching was complete. Only one further hatching, which was of minor proportions, occurred (Macoah Passage-Stopper Islands Sector on April 30).

The sampling of April 26–30 showed a general decrease in numbers of larvae in all sectors but one. About twice as many larvae were taken in the Chrow Island Sector (G), on April 26–30 as during the previous period (410 and 206 larvae per haul, respectively), indicating a continuing seaward movement of larvae along the northwest shore of the Sound.

By May 7–11, the numbers of larvae decreased further. In all sectors, except that of Nettle Island (D) where the most recent large hatching occurred, the average haul contained fewer than 100 larvae.

In the Toquart Bay and Hankin Island Sectors (A and F), larvae were particularly few on April 26–30. In the former Sector, the abundance had been low since April 16, but high numbers were recorded in the latter Sector during the period of May 7–11.

From May 26–30, the sampling hauls failed to catch appreciable numbers of larvae in any sector. In a total of 56 hauls, only 5 larvae were taken.

FACTORS AFFECTING THE HORIZONTAL DISTRIBUTION OF HERRING LARVAE

In the preceding section, the distribution of herring larvae in the northern part of Barkley Sound was described. Consideration will now be given to the factors that control larval distribution.

One factor of obvious importance in the distribution is the location of the spawnings. The distribution pattern consistently shows high early abundance in the vicinity of spawning grounds. Inasmuch as time as well as space is an aspect of distribution, the time of spawning is also a factor. Also, since abundance of larvae is also a consideration in describing distribution, the magnitude of the spawning is also involved. The influence of each of these aspects of spawning was shown in the foregoing description of the distribution of larvae in the northern part of Barkley Sound.

The location, time, and extent of spawning do not alone explain adequately the pattern of distribution. Large concentrations of larvae were found at considerable distances from spawning grounds. Did they actively migrate or were they carried, and, if the latter, what were the mechanics of transport?

Planktonic Nature of Herring Larvae

First, it seems desirable to consider whether herring larvae are planktonic, that is, whether they drift more or less passively with water movement.

One source of evidence for their planktonic behaviour is the fact that they are readily collected along with various forms of plankton in horizontal tows of nets. Up until a standard length of 21 or 22 mm was reached, larvae could be readily captured in this way, and on numerous occasions larvae were taken which showed that metamorphosis had begun. However, after the length exceeded about 22 mm, there were strong indications of a certain amount of evasion of the sampling nets by larvae. The presumed evasion may be linked with the development of a tendency towards free swimming and schooling.

Further evidence of the planktonic existence of herring larvae has been gained through direct observation of larvae in surface waters on dark nights. Newly-hatched larvae and larvae averaging slightly over 20 mm have been observed. In each case, their movements outlined by the phosphorescence of certain algae and copepods have appeared random in character.

The belief that herring larvae are planktonic, at least up to the onset of metamorphosis, is widely held by European investigators (Wallace, 1924; Johansen, 1927; Mielck, 1929).

Water Movements in Northern Barkley Sound

In April, 1950, the net flow of water over a period of 25 hours (1 tidal cycle) was determined at the surface, and at depths of 3, 5, and 10 fathoms (5.5, 9.2, 18.3 m) for several places in northern Barkley Sound (Doe, 1952). The results are shown in Fig. 13 and Appendix 16.

Three general patterns of flow were determined from the oceanographic data. They are shown schematically in Fig. 14.

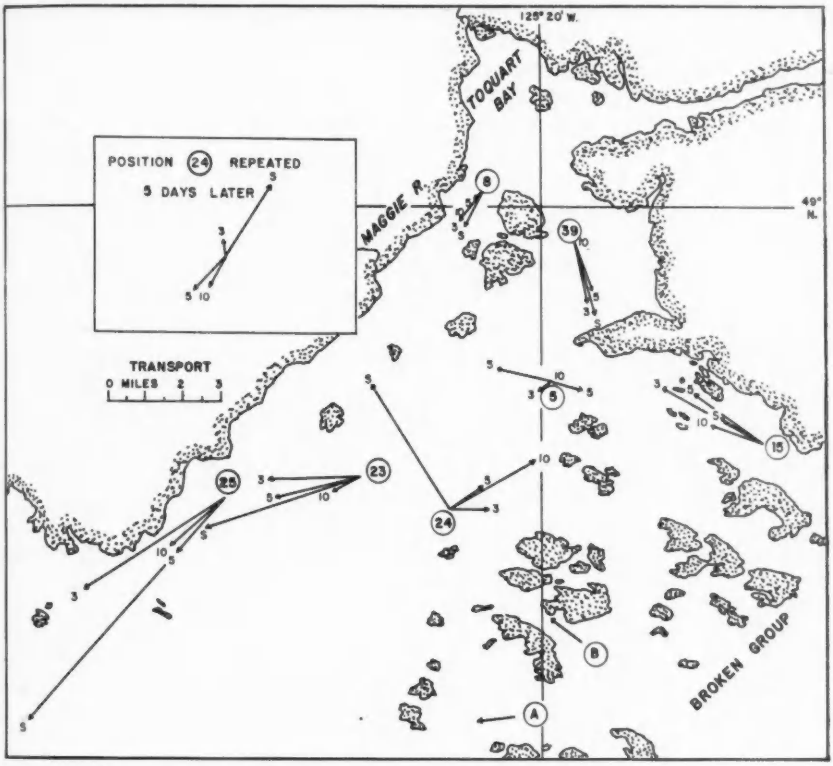

FIG. 13. Net flow in 25 hours (tidal day) observed at oceanographic stations in Barkley Sound in April 1950 at the surface (S), and at depths of 3, 5, and 10 fathoms; after Doe, 1952. Direction of vectors indicates direction of flow, and length of vectors represents amount of net flow. At oceanographic stations A and B vectors show the direction only of the flow at the surface (from data taken in 1937).

SEAWARD FLOW

Strong seaward movement of water at all depths occurred along the northwest coast of the Sound. At Station 8 at the mouth of Toquart Bay, the average movement towards the open sea for all depths was 0.8 nautical mile (1.5 km) per tidal cycle (25 hours), and at Station 25 near the mouth of Barkley Sound the average movement seaward was 4.0 miles (7.4 km). The movement at the surface was greater than below the surface at each station.

This current pattern is, at least in part, a result of the runoff from the Toquart and Maggie Rivers which empty along the northwest coast of Barkley Sound. In accordance with the Coriolis force their discharge would be expected to veer to the right and move towards the sea. The salinity pattern observed by Doe (1952) shows clearly that this is what happens. A distinct salinity gradient was found from 15‰ at the mouth of Toquart Bay to 26‰ at the mouth of the Sound.

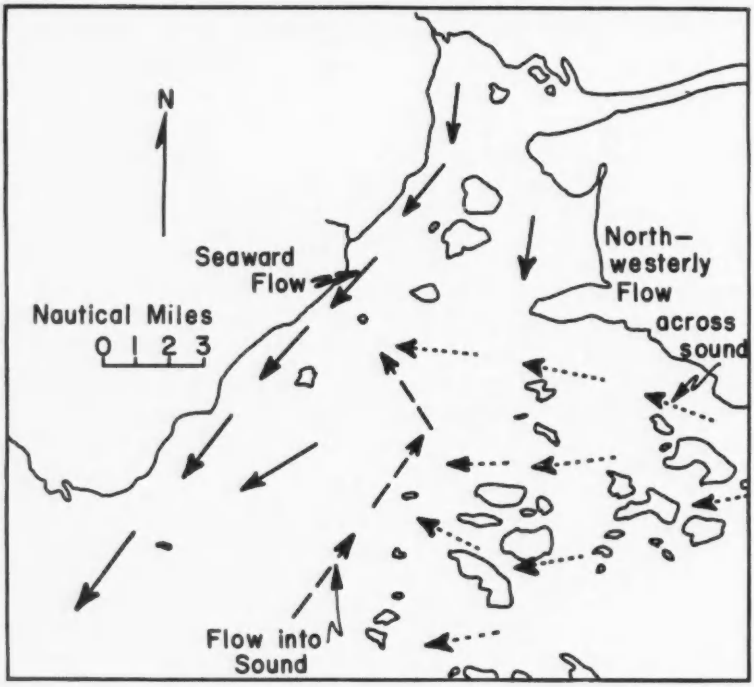

FIG. 14. Map of the northern part of Barkley Sound showing schematically the direction of flow of the three main currents; adapted from data in Fig. 13. *Solid arrows*: seaward flow along the northwest coast of the Sound. *Dotted arrows*: northwesterly flow across the Sound. *Dashed arrows*: flow into the Sound.

NORTHWESTERLY FLOW ACROSS THE SOUND

At Nettle Island (Station 15) and at one point in the islands of the Broken Group (Station B), the water moved across the Sound in a general northwesterly direction. Doe (1952) showed that this current pattern was directly related to the discharge of the Somass River at the head of Alberni Inlet. A pronounced salinity gradient extended from the mouth of Alberni Inlet across Barkley Sound (from 8.5 to 27‰).

FLOW INTO THE SOUND

On April 19 at Oceanographic Station 24 (near Hankin Island), water movement at the surface and at all depths was from the open sea into the Sound. A repeat set of observations made 5 days later still showed a strong movement of surface water flowing from the open sea, but at depths of 5 to 10 fathoms (9.2–18.3 m) a moderate seaward flow was indicated.

The net onshore movement of water in this portion of Barkley Sound is interpreted as a compensating current for the net offshore movement of water caused by the two seaward-moving currents previously described. Tully (1952) has shown that the fresh water discharge from rivers entering the sea moves seaward over the underlying ocean water, forming a brackish upper zone in which salinity continually increases with depth and distance seaward along the line of flow. The seaward movement of ocean water (mixed with fresh water) in the upper zone is compensated by a counter inflow of ocean water in a lower zone. Doe (1952) points out that this general situation is somewhat modified in the northern part of Barkley Sound. As shown previously, ocean water at all depths moved seaward in some places (Fig. 13), and instead of the compensatory flow from offshore being underneath the seaward-moving current it was moved laterally to another location (Fig. 14).

Water movement at Station 39 (in Mayne Bay) and at Station 23 (about 2 miles southeast of Forbes Island) appears to be most closely related to the pattern of seaward flow noted along the northwest coast. Currents at Station 5 (to the south of Mayne Bay) are apparently mainly under the influence of the northwesterly flow across the Sound, but there are indications that the movement of water in this area is affected to some extent by the movement of water from offshore.

Doe (1952) considered the effect of tides on the current pattern. He found that the flood tide tended to decrease the seaward flow along the northwest shore of the Sound by bringing salt water inshore from the open sea, and that the ebb tide carried with it fresh water discharged from the rivers that had accumulated during the period of the flood tide. With the next turn of the tide to flood, part of the body of relatively fresh water was detached and floated away as a "cloud" until dissipated, while the rest of it was swept back into the Sound.

Distribution of Larvae in Relation to Water Movements

Transport of larvae along the northwest shore

If herring larvae are planktonic and subject to being readily transported by water currents, it would be expected that the currents shown to exist in the northern portion of Barkley Sound would have a marked effect on the distribution of the larvae, described in a previous section.

The strong currents along the northwest shore of the Sound would account for the transport of larvae observed in 1951 (Fig. 10) from the head of Toquart Bay to the mouth of the Bay, and later to the vicinity of the Stopper Islands. These currents would also explain the movement of larvae in 1950 (Fig. 12) from the Toquart Bay and Macoah Passage Sectors to the Forbes Island Sector (April 13–15) and to the Chrow Island Sector (April 18–20).

A rough approximation can be made of the length of time necessary for larvae to be transported along the northwest shore on the assumption that average speed of water transport was about equal to that observed at Oceanographic Station 6 in Toquart Bay on April 21–22 (Appendix 16). Since the distances from the Stopper Islands to Forbes Island and to Chrow Island are $3\frac{1}{2}$ and 7 miles (6.5 and 13 km), respectively, and since the average speed of flow was about 0.8 mile per day, the time necessary to reach Forbes Island would be about 4 days, and to reach Chrow Island about 9 days. The peak of spawning in the Macoah Passage-Stopper Islands Sector occurred about April 7. By April 13 (6 days later), large numbers of larvae were found in the Forbes Island Sector, and by April 18 (11 days later) larvae were abundant in the Chrow Island Sector. Sampling of larvae was not carried out every day in these sectors, and therefore increased abundance may have occurred a day or two prior to sampling.

Low abundance of larvae in the outer portion of the Hankin Island Sector

In describing the distribution of larvae in 1950, an area containing relatively few larvae was noted in the outer section of the Hankin Island Sector in the April 13–15 and April 18–20 periods (Fig. 12). This area was closer to the main hatching areas (in the Macoah Passage-Stopper Islands and Toquart Bay Sectors) than another area (the Chrow Island Sector) to which large numbers of larvae had moved.

This situation can apparently be explained by the different current pattern that prevailed in the Chrow Island and outer Hankin Island Sectors. Instead of a seaward movement of water, an onshore current was dominant in the latter area. Thus, no direct means of transport was afforded larvae from the main hatching region to the outer Hankin Island Sector.

A few days later (April 21–25) large numbers of larvae were found around Hankin Island (Fig. 12). Length frequency data showed, however, that these larvae were not derived from spawnings on the northwest coast of the Sound, but rather from recent hatching of a spawning in the Nettle Island Sector. Oceanographic data showed that the waters of the latter area were under the influence of a third current pattern, which moved the waters in a northwesterly direction across the Sound. Thus, it appears that the larvae from Nettle Island were carried through the islands of the Broken Group in the direction of Hankin Island.

Effect of the tide on larval distribution

In addition to the effect of major water movements on the distribution of larvae (described above), the action of tides can be shown to influence distribution. Two main effects have been noted: (a) the action of the tide in carrying newly-hatched accumulations of larvae from the spawning ground into the bay, and (b) the effect of the tide on the movement of the larvae between the head and the mouth of a bay.

Segregation of newly-hatched larvae by tides. A striking effect of tidal currents on larval distribution was noted by the presence of two distinct groups of larval herring in Toquart Bay from March 24 to 26, 1951 (Appendix 13). Through the action of the flood tide, larvae were presumably held over the spawning grounds after hatching. Then, with the change to ebb tide, the accumulated larvae were quickly carried out into the Bay. The concentration of larvae carried into the Bay would not necessarily be carried back over the spawning grounds at the next flood tide, since various other factors besides tidal currents (freshwater discharge, winds, salinity gradients) affect the movement of the water. It would not be expected, however, that such groups of larvae could maintain their identity for long. Four days later, when sampling in Toquart was resumed, significant differences between larvae in different samples could not be distinguished. The early groups were thoroughly incorporated into the general brood, and the widespread distribution of larvae over the entire Bay precluded the segregation of newly-hatched accumulations.

DISTRIBUTION OF LARVAE DURING DIFFERENT STAGES OF THE TIDE. The effect of the tide on the distribution of larvae in Toquart Bay was shown by sampling at two places in the Bay during different stages of the tide. One of the stations was located in the centre of the Bay and the other at the mouth, with a distance of about ¾ mile (1.4 km) separating them. Samples were taken at the surface of the water at both stations when the tide was high (during the night of April 2–3, 1950) and when the tide was low (during the night of April 4–5, 1950). The results are shown in Table IV.

TABLE IV. Average numbers of larvae taken in surface Samples at the centre and at the mouth of Toquart Bay at high tide on April 2-3 and at low tide on April 4-5, 1950. Number of samples is shown in parentheses.

Location	Number of larvae per sample	
	High tide[a]	Low tide[b]
Centre of bay	1250 (1)	3120 (3)
Mouth of bay	266 (2)	4275 (2)

[a] High tide at 00:25 hours; samples taken at 00:30 hours.
[b] Low tide at 19:37 hours; samples taken at 20:00 hours.

Because the number of samples was small and since two days elapsed between times of sampling, the results cannot be considered conclusive. However, the fact that (1) about 5 times as many larvae were taken in the centre of the Bay as at the mouth after the flooding of the tide, and (2) about 1/3 more were taken at the mouth than in the centre after the ebbing of the tide, suggests that the differences in distribution were largely the result of the action of tidal currents.

Visual evidence of the effect of the tide on the distribution of older larvae (18 to 26 mm in length) was obtained in Whitepine Cove on the night of May 18, 1947. The larvae could readily be seen near the surface of the water by the phosphorescence caused by their movements, and hence their distribution in the Bay could be generally followed through the night. Between 22:00 and 23:00 hours (high tide was at 23:03 hours), their distribution was restricted to an area at the head of the Bay. After the tide had ebbed for about 3 hours, the body of larvae had moved beyond the centre of the Bay and they appeared to be less concentrated.

Intensive sampling at a station near the head of Toquart Bay throughout the night of April 8–9, 1950, gave a further indication of the effect of the tide on the distribution of larvae (Fig. 15). After dusk, the tide was nearly high and large numbers of larvae were found in the surface waters. About 20,000 larvae per tow were present in the upper fathom (1.8 m) of water, as compared to 300 at a depth of 3 to 4 fathoms (5.5–7.3 m). During the next hour, the ebb tide was at its greatest rate of flow, and the surface waters bearing the high concentration of larvae would be expected to have moved towards the mouth of the Bay. When sampling at the head of the Bay was resumed at 21:00 hours, larval abundance in the surface layer had decreased, and it remained at a relatively low level

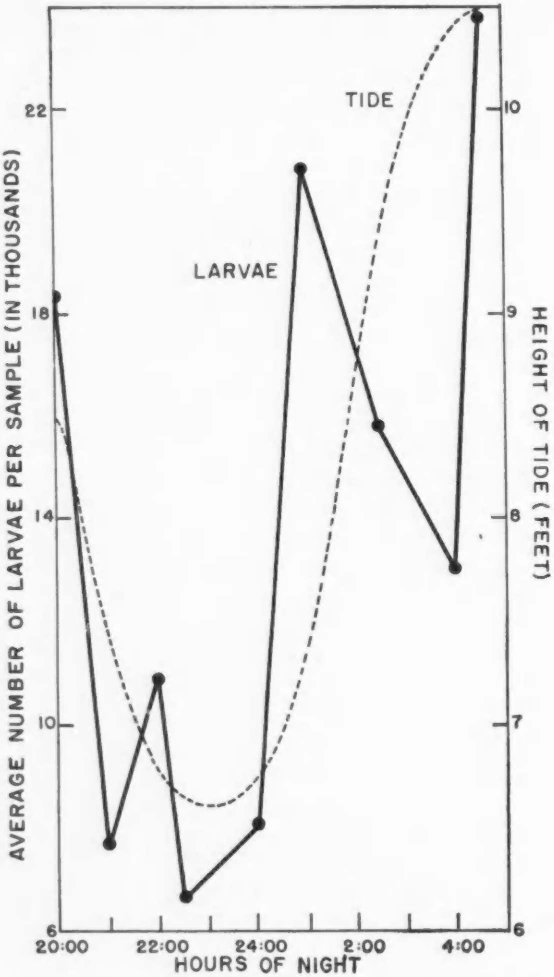

FIG. 15. Concentration of larvae (surface samples) in relation to tidal height at the head of Toquart Bay on the night of April 8–9, 1950.

(about $\frac{1}{2}$ of that noted after dusk) until the tide began to flood. When high tide was reached at 05:00 hours, the number of larvae in the surface layer was greater than it had been at any time during the night. At no time during the night did the samples at a depth of 3 to 4 fathoms contain more than 1/10 the number of larvae found in surface samples.

It would therefore appear that during the night the tide shifted the body of larvae from the head of the Bay towards the mouth and brought it back again. Length frequency data suggested that few, if any, newly-hatched larvae were added to the main brood throughout the night.

Samples taken during the time that the rate of flow of the flood tide was greatest (from about 01:00 to 04:00 hours) showed considerable variation in numbers of larvae. A possible explanation of the low numbers of larvae in some samples taken after 02:00 hours is that vertical mixing of the water by the fast flooding tide had temporarily removed large numbers of larvae to deeper levels.

SURVIVAL OF HERRING LARVAE

Probably the most striking feature of larval distribution is the inevitable decrease in abundance with time after hatching. From this fact emerge certain questions. What is the extent of this decrease? What are the causes? Are the factors that cause decrease in numbers of larvae from a particular area factors which affect the survival of the larvae of the entire population?

To examine these questions, the decrease in numbers of larvae in Toquart Bay in 1950 will be examined, and the possible effect of various factors on the survival of larvae will be discussed.

Decrease in Abundance of Larvae in Toquart Bay in 1950

The abundance of larvae in Toquart Bay in 1950 is plotted logarithmically in Fig. 16 for 5-day periods from April 1–26. To assist in interpreting the nature of the decrease, the modal lengths of larvae are shown for each day of sampling in Fig. 17.

In the first 10 days of April, a large amount of hatching occurred, with larval abundance reaching a peak in the period of April 6–10. During this time, the length of larvae in the samples generally increased as a result of growth, but considerable variation occurred in mean and modal lengths from day to day. The variation resulted from the addition of newly-hatched larvae to the general body of larvae in the Bay and from incomplete mixing of the various daily hatchings.

After April 6–10, the amount of hatching in Toquart Bay was relatively small and the larvae decreased in numbers at a more or less steady rate until April 26–30, when an average of only 3 larvae per sample was obtained (Fig. 16).

Abundance increased from April 26–30 to May 6–10. It was not possible to determine definitely whether the new addition of larvae was derived from spawnings in Toquart Bay or from spawnings outside the Bay. No spawnings were reported in Toquart Bay in late March or early April, but the numbers of larvae indicated that the spawnings were small and they might have occurred

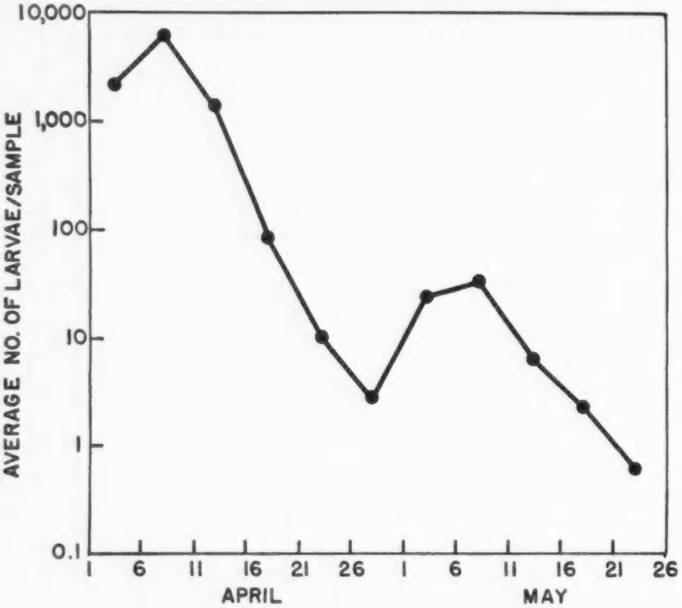

FIG. 16. Abundance of larvae in Toquart Bay in 1950 during successive 5-day periods after hatching.

in the Bay without having been observed. It appears more likely however that the larvae were hatched from small spawnings which occurred on March 27 in Mayne Bay and near the Maggie River, and were subsequently carried into the Bay.

No further hatching occurred after May 6–11, and larval abundance decreased at a fairly constant rate.

Study of the modal length of larvae obtained on each day throughout the sampling period (Fig. 17) showed that larvae of different size were frequently taken on the same day. The data suggested that three growth lines could be drawn, presumably representing three larval broods of different age. The abundant early-hatched brood (Fig. 17—line A) and the much smaller second brood (line B) reached a length of 20 mm on about May 12 and May 16, respectively. The third brood (line C) attained a length of 17 mm on about May 16.

Extrapolation of the growth trends of each brood indicated that because of the accelerated growth of later broods, the larvae of all broods would begin to metamorphose at about the same time. As pointed out previously, sampling methods failed to take larvae after they had reached about 20 mm.

The rate of decrease in the numbers of larvae in Toquart Bay in 1950 apppeared to be relatively constant, both for the original brood and for later-hatched broods (Fig. 16). For the former, the average rate of decrease was calculated at 34% per day (Appendix 17), which would involve a reduction of almost 99.98%

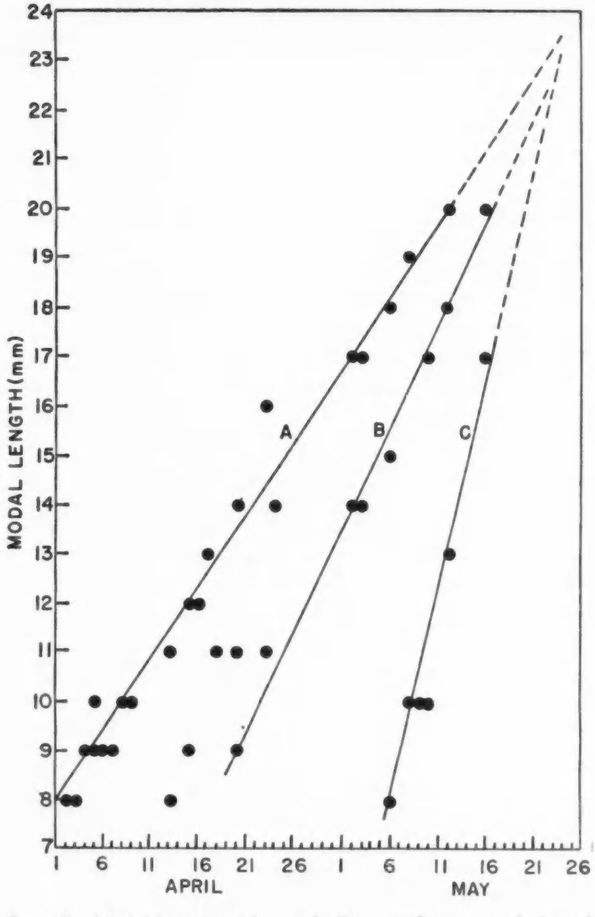

FIG. 17. Modal lengths of larvae in Toquart Bay on each day of sampling in the spring of 1950. Lines A, B, and C are presumed trend lines for growth of three successive broods; trend lines were fitted visually.

in numbers of larvae in the 20-day period during which sampling showed decreasing abundance. The average rate of decrease in later-hatched broods was 22% per day.

FACTORS INVOLVED IN SURVIVAL OF LARVAE

What does the estimated extent of decrease in numbers of larvae in Toquart Bay mean in relation to the survival of the entire larval brood of the population? Assuming that the situation observed in Toquart Bay is representative of that in other spawning localities, the question arises as to what is the fate of the larvae which disappear. Do they all die? It has been shown that much of the decrease in abundance is due to transport from the inshore areas by water currents. Do these larvae, thus transported, die?

Analysis of the mortality shown to occur in other stages of the life-history suggests that all larvae transported from spawning localities do not die. It has been calculated (Stevenson, 1955b) from data on the mortality of herring during the incubation period (Outram, 1958) and in the period of adult life (Tester, 1948) that the average larval mortality is about 99.5%. (Even if considerable errors were involved in the determination of mortality in the various stages of the life-history, the analysis indicated that the estimate of average larval mortality would not likely vary beyond the range of 98.9 to 99.7‰). The decrease in numbers of larvae from a brood area (Toquart Bay) was estimated at about 99.98‰. If, therefore, the mortality of Toquart Bay larvae approximates that of the combined larval broods of the population, it would appear that not all of the decrease in numbers of larvae in the brood areas is a result of mortality. This would suggest that not all larvae that are carried from brood areas die.

Possible factors involved in mortality of larvae will be discussed under two headings, namely (1) factors that directly cause death, and (2) the possible operation of these factors as a result of larvae being transported out to sea.

Causes of mortality in the vicinity of spawning grounds

Predation. Instances of predation on herring larvae were found in each year of the study. Most information was obtained on the predation caused by certain macroplankters which were taken along with herring larvae in the samples. The ctenophores (*Pleurobrachia* spp.) appeared to be the greatest predators, with jellyfishes (numerous species) and chaetognaths (*Sagitta* sp.) following in that order of importance.

As many as 45% of the larvae in a sample had been or were being devoured by ctenophores. This was calculated by counting the number of ingested as well as non-ingested larvae in the samples. Some ctenophores were found with two larvae being eaten at the same time. While some of the predation may have occurred within the collecting gear, these instances strongly suggest that heavy predation does at times take place. On one occasion in Mayne Bay in 1947, when ctenophores were so numerous that they appeared to form a false bottom at a depth of about 2 fathoms, heavy predation on larvae was observed. This practically solid mass of ctenophores was found at about the same depth during the day and at night. Since many larvae in the course of diurnal migration would probably pass through the depth at which the ctenophores were concentrated, severe mortality must have occurred. Other investigators, including Jensen (1950) and Bückmann *et al.* (1953), have made reference to the predation of ctenophores on herring larvae.

However, although predation by ctenophores, jellyfish and chaetognaths is probably severe within certain larval broods, it seems unlikely that predation is generally a serious source of larval mortality. In almost 4000 larval samples, evidence of such mortality was found in fewer than 100 samples.

STARVATION. No studies were made on the food of herring larvae in the present investigation. European investigators have, however, devoted much attention to the subject, and have determined in considerable detail the type and quantity of food consumed by herring larvae at various stages of development (Lebour, 1924; Hardy, 1924; Jespersen, 1928; Marshall *et al.*, 1937). Ogilvie (1927) and Marshall *et al.* (1937) observed an increase in food intake after the onset of metamorphosis. This suggests that lack of food could be a limiting factor in survival at that time. It has, however, been impossible to test this possibility because of the difficulty of obtaining quantitative estimates of the abundance of young herring immediately before the onset of metamorphosis. Various workers, in addition to the writer, have found evidence that larvae tend to escape the sampling gear at this stage of development.

Rollefsen (1951) and Bückmann (1950a) emphasized that food is probably a critical factor in survival of herring larvae immediately after the absorption of the yolk sac when feeding commences. Lebour (1921) and Hardy (1924) pointed out that even before the yolk sac is absorbed, some food is taken, but apparently the amount is relatively small. Schach (1939) found in experiments that larvae took no food until 3 or 4 days after the absorption of the yolk sac, but this may have been a result of the unnatural conditions under which they were kept in the laboratory.

The view that large-scale mortality might occur immediately after the yolk sac stage has been considered in relation to data collected in the present study. Most of the samples taken in the early period of larval life have been shown to be unsuitable for this analysis because of a long period of hatching and because of extensive dispersal from the immediate area of hatching. However, larvae sampled in Queen Cove (on the upper west coast of Vancouver Island in 1949) were found to have mostly hatched within 3 days, and relatively little dispersal from the Bay occurred in the first 2 weeks after hatching. The rate of decrease of larvae in this locality is shown in Fig. 18 and Appendix 18, along with the decrease in percentage of larvae bearing yolk sacs and the increase in growth over this period.

If it can be assumed that the sampling was sufficiently intensive to give a true indication of the decrease in numbers of larvae during the period, the results can be interpreted as indicating that no drastic decrease in abundance occurred from the time that larvae with yolk sacs comprised 91% of the samples (March 31) until the time that no larvae with yolk sacs were found (April 18). The data therefore suggest that in Queen Cove in 1949 lack of suitable food was probably not a critical factor in the survival of larvae. There is the possibility, however, that this is not always the case in other areas or in other years.

SALINITY. Herring larvae can withstand, at least for a short time, very great changes in salinity. In 1951, considerable numbers of larvae were taken in Toquart Bay in water ranging in salinity from 1.4 to 28.0‰. Bückmann (1950b) found larvae in water with a salinity as low was 10‰, and he considered they could be taken in less saline water. Fujita and Kokubo (1927) showed experimentally that herring larvae could live for at least a time both in normal sea water (32.2‰) and in fresh water.

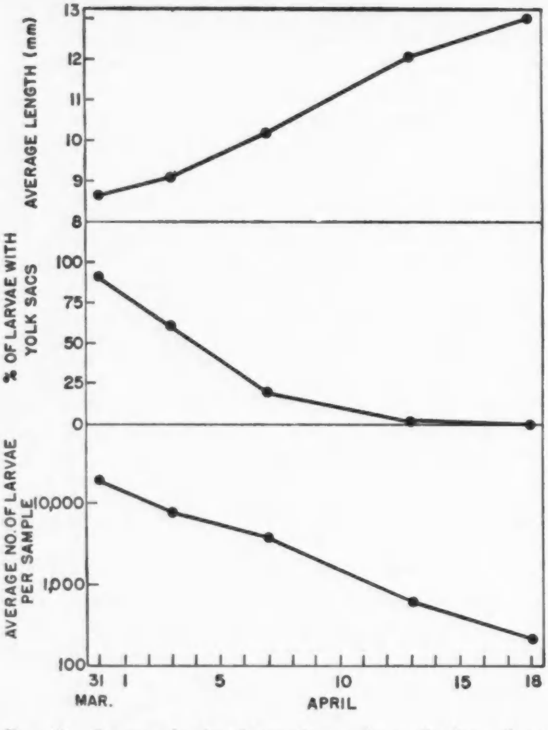

FIG. 18. Decrease in abundance of young larvae in Queen Cove in the spring of 1949, showing decrease in percentage of larvae with yolk sacs and increase in average length of larvae.

Fujita and Kokubo (1927) carried their experiments further to determine survival of herring larvae in water of different salinities. They found that greatest survival occurred in water of 4/5 normal salinity (25.8‰), and poorest survival in normal sea water (32.2‰). A salinity of 19.4‰ gave the next greatest survival after 25.8‰, and this was followed by 13.0‰, 6.8‰, 3.4‰ and fresh water. On the basis of these results, the surface waters of the northern part of Barkley Sound would appear to be favourable to the survival of herring larvae. Doe (1952) found that the range of surface salinity was from 15 to 29‰ on April 4, 1950, and from 22 to 26‰ on April 25, 1950.

TEMPERATURE. In 1951, the surface temperature of the water was taken at the time of sampling for larvae. The range of temperatures encountered in Toquart Bay and vicinity was from 7.8 to 15.3°C. Considerable numbers of larvae were taken in water of from 9.5 to 13°C; by the time that the temperature was greater than 13°C, larval abundance had decreased as a result of dispersal and the effect of mortality.

Marshall *et al.*, (1937) found experimentally that the movements of herring larvae increased with increase in temperature to 23°C, but that they became sluggish at higher temperatures. Kotthaus (1939) in similar experiments considered that larvae could survive at a temperature of 25.5°C. Little data are available on the preferred temperatures for herring larvae. Kotthaus (1939) suggested that the optima were probably between 10 and 20°C. There seems little likelihood that the temperature of the water in Barkley Sound ever becomes so high or so low as to affect survival of larvae directly.

Temperature may, however, have an indirect effect upon survival through its influence on the duration of the larval stage. Figure 17 indicates that larvae hatched early grow more slowly than those hatched later in the spring. Kotthaus (1939) found that the rate of development was decreased at low water temperatures—in water of 12.8°C the yolk sac of herring larvae disappeared in 3 days, while at 10.3°C it disappeared in 7 days. The early larval broods of the spring would therefore have a longer period of larval life than late broods, and the various mortality factors would act on the former over a longer period of time. Similarly, years in which the springs are colder than average may tend to reduce survival below that of warmer springs.

SUMMARY. The data on which the foregoing analysis of the mortality factors of herring larvae is based are rather sparse. It may be significant, however, that none of the various factors, either singly or considered together, appear to be capable of causing the very great mortality (over 99%) which occurs in the period of larval life.

EFFECT OF WATER TRANSPORT OF LARVAE ON SURVIVAL

RELATION BETWEEN LARVAL DISTRIBUTION AND CURRENT PATTERN. Transport, in itself, is unlikely a factor in mortality of larvae. Large numbers of larvae were found which had evidently been transported several miles from the area of hatching. It could be, however, an indirect means of major mortality, if larvae were transported to areas where predation, lack of food, or physical characteristics of the water were inimical to survival.

In the discussion of the distribution of larvae in the northern part of Barkley Sound in 1950, the transport of larvae along the northwest shore of the Sound was followed to the Forbes Island Sector and later to the Chrow Island Sector at the mouth of the Sound (Fig. 12). Oceanographic data indicated that larvae carried along the northwest shore would be carried at a progressively greater speed as they reached the mouth of the Sound (Appendix 16). The net transport from the Chrow Island Sector to the open sea was found to be at the rate of about 7.7 nautical miles (14.3 km) per day in the surface waters where the larvae were found to be densely concentrated at night. It is evident that such extensive transport would disperse the larvae from the main spawning grounds of Barkley Sound (and, therefore, of the herring population under consideration) far out to sea.

Relatively few of these larvae apparently return to the waters of the Sound. The oceanographic study showed that the return current into the Sound was in the vicinity of the outer Hankin Island Sector (Fig. 13 and 14). In this

Sector, the numbers of larvae derived from the main spawning grounds along the northwest shore of the Sound were relatively small, suggesting that few larvae carried to the mouth of the Sound returned in the compensatory inflowing current.

EVIDENCE THAT LARVAE TRANSPORTED TO SEA DO NOT SURVIVE. By elimination of other possibilities, it appears that the larvae which do not return to the waters of the Sound do not survive, and that this is the main component of the vast mortality occurring in the larval period of the life-history.

No direct evidence is available to indicate that most larvae carried to sea do not survive, but there are several sources of indirect evidence. While none of these pieces of evidence is conclusive, they strongly support the contention, when considered together.

1) No larvae were caught in 75 net hauls and pump samples taken off the mouth of Barkley Sound. Considering the vastness of the area and the relatively small amount of water sampled, this does not necessarily mean that larvae do not exist there. On the other hand, the complete failure to capture a single larva may well indicate that those that were carried offshore died.

2) Even if it were assumed that larvae could survive in the open sea, they might still be lost to the population from which they were derived. Many days (or perhaps weeks) would elapse before they would metamorphose, depending on their stage of development on entering the sea, and on the temperature of the water. By this time, they would be drifted long distances out to sea and along the coast to areas of other populations or beyond the areas where herring occur. When the time for schooling occurred, each individual would be widely separated from another individual. While it is possible that they could survive as isolated juveniles in the open sea or that they could return singly to the inshore waters from which they originated, such a possibility seems highly improbable.

3) No large quantities of recently-metamorphosed juvenile herring have been found in offshore waters or in bays or inlets more than a few miles from major spawning grounds in 4 years of search (Hourston, 1958, 1959). It could be argued with some justification that schools of juveniles would be difficult to detect in the rough waters offshore. On the other hand, it appears significant that numerous schools are consistently found soon after metamorphosis in the vicinity of the spawning grounds—for example, in Toquart Bay, Mayne Bay, and near the Stopper Islands.

4) As discussed previously, Fujita and Kokubo (1927) found experimentally that normal sea water (32.2‰) is less favourable to survival of herring larvae than water of less than normal salinity. Assuming that these results are applicable to conditions in nature, less survival of herring larvae would be expected offshore than in Barkley Sound. Fujita and Kokubo considered that their results explained "why fry thrive better in an estuary than on the high sea".

Fujita and Kokubo gave no indication of how unfavourable salinity causes death. Whether it acts directly on the larvae or whether it affects their tolerance to temperature or some other factor is not known. The possibility exists that food necessary for the survival of larvae is not found in water of high salinity.

Hjort (1926) theorized that survival of herring may be affected by young herring being carried out to the open sea where insufficient plankton is available.

5) In spite of the fact that Atlantic herring generally spawn offshore in highly saline water (as contrasted with the spawning of Pacific herring along shore near the mouths of rivers), the larvae at an early age are found in coastal waters of low salinity. In studying larval distribution in the North Sea, Wallace (1924), Lissner (1927), Schnakenbeck (1927), Mielck (1929), and Bückmann (1950a) concluded that the tremendous quantity of herring larvae found on the coasts of the North Sea during the spring and summer were largely derived from the major spawning grounds on offshore banks. They explained the inshore movement of the larvae by water currents. Mielck (1929) suggested that those larvae that did not reach the coast did not survive. Bückmann (1950b) stated that the inshore movement occurred relatively quickly and that metamorphosis and schooling did not occur until the larvae reached the brackish waters close to river mouths.

These results of research on the larvae of Atlantic herring suggest that the habits of Pacific and Atlantic herring are essentially similar in the larval stage, and although conclusive proof is lacking, a strong possibility exists that the larvae of both species of herring do not survive in the open sea.

High salinity does not apparently affect the survival of newly-hatched larvae of Atlantic herring, since hatching is known to take place on various banks of the North Sea in water of 34‰ salinity. McMynn and Hoar (1953) have shown that the incubation, hatching, and early development of larvae, at least up to the absorption of the yolk sac, also proceed normally in Pacific herring in water of a salinity of 34‰. Thus, while less than normal salinity enhances survival of older larvae (Fujita and Kokubo, 1927), the newly-hatched larvae do not require an environment of which low salinity is a characteristic. It is of interest in this regard that Ford (1929) has found that hatching and early development of Atlantic herring occur normally in water of salinity equal to or lower than that in which these processes take place naturally in Pacific herring.

YEAR-CLASS STRENGTH DETERMINED BY LARVAE REMAINING IN SOUND. If few of the herring larvae carried to sea survive, it follows that the strength of the year-class is largely dependent upon that relatively small number of larvae that remain in the Sound during the period of planktonic existence (and to a much less degree on the few larvae that are carried back into the Sound by the inflowing compensatory current). Since, as pointed out previously, no newly-metamorphosed schools of juvenile herring are found except in the vicinity of the spawning grounds, it appears reasonable to conclude (1) that these schools are mainly derived from those larvae that remained in the Sound, and (2) that they represent the year-class which in future years will be recruited to the adult stocks of the population.

On the assumption that the larval period is the most critical in the life-history, it would be expected that the number of herring eventually recruited to the adult stocks would be more or less proportional to the number of juvenile herring. An indication that such a relationship may exist was given by the fact that the strong 1947 year-class on the lower west coast of Vancouver Island (Fig. 3) was represented by numerous schools of juvenile herring observed in the summer of 1947, while the weak 1948 year-class was represented in the summer of 1948 by very few juvenile schools (Stevenson and Lanigan, 1950; Stevenson *et al.*, 1951). A similar relationship has also been observed in subsequent years (Hourston, 1958, p. 948).

METEOROLOGICAL FACTORS AND YEAR-CLASS STRENGTH

General Considerations

In the preceding section, evidence has been put forward to substantiate the proposition that dispersal of herring larvae to sea is the chief cause of larval mortality. In another paper (Stevenson, 1955b), the writer has demonstrated that the greatest mortality occurring in the life-history of the herring takes place during the larval period. It would appear, therefore, that the abundance of a year-class probably depends upon differences from year to year in the numbers of larvae carried out to sea.

This reasoning has suggested the desirability of comparing the strengths of year-classes on the lower west coast of Vancouver Island (Fig. 3 and Appendix 2) with the extent of dispersal of larvae from Barkley Sound out to sea. Since direct estimates of the extent of larval dispersal are available for only one year (1950), other means of obtaining an index related to dispersal of larvae have been sought. Information on the year-to-year variations in net transport of the water in Barkley Sound, or data on the annual variations in the runoff of the Maggie and Toquart Rivers would give promise of providing a suitable index, but it has not been possible to obtain either of these types of data. Net movement of the currents was obtained only in 1950, and no quantitative data were available on the runoff of rivers of the northwest coast of the Sound. Data are available on the runoff of the Somass River at the head of the Alberni Inlet, but they were taken for relatively few years; also, there is some doubt that the discharge of this river would be indicative of the runoff of rivers along the northwest coast of the Sound.

Emphasis has, therefore, been placed on obtaining information on meteorological factors which probably influence river discharge and current flow. Several closely-related factors would appear to be involved. The most obvious factor influencing river discharge is precipitation. Air temperature is also a factor, since precipitation falling on the drainage basin in the form of snow would have a delayed effect upon river discharge. Tully (1937) has indicated the possible influence of winds on current flow. He pointed out that northwest winds on the west coast of Vancouver Island affect offshore currents in such a way as to increase the offshore flow of waters from the sounds along the coast. Conversely, it might be expected that dominant southeasterly winds would "pile up" waters in the sounds and slow down seaward movement of the surface layers.

These considerations would lead to the conclusion that dominant southeast winds (tending to hold surface waters in the sounds) and low precipitation (giving low river runoff) would tend to reduce seaward movement of surface waters and therefore transport of larvae to sea, and hence to favor year-class survival. However, there is a complicating feature involved, namely, that the weather pattern[5] of the area is such that northwest winds (unfavorable to larval survival) are generally accompanied by partly clear or clear skies, and low precipitation (favorable to survival), whereas southeast winds (favorable to survival) are characteristic of cloudy skies and heavy precipitation (unfavorable to survival). Added to this is the fact that late March and the month of April constitute a transitional period from the winter weather pattern of southeast winds and heavy precipitation to the summer pattern of northwest winds and low precipitation. In certain years, the winter pattern predominates during this period, in other years the summer pattern predominates; but in each year highly variable weather conditions exist.

In view of the complicated interrelations between the various meteorological factors and because of the differences in the indirect effects of the various factors on net transport of inshore waters, a simple relationship between them and year-class strength would not appear likely to exist. In point of fact, most comparisons attempted between a single meteorological factor and year-class strength have not shown a close relationship. However, the possible importance of snowfall in determining year-class strength appears worthy of special attention.

Snowfall and Year-Class Strength

Two possible explanations may account for the lack of a relationship between precipitation during April and the eventual abundance of the year-class which in that month exists as larvae. The favorable effects of low precipitation may be countered by the unfavorable effects of northwest winds which (as mentioned before) are characteristic of low precipitation, and *vice versa*. It may also be that the amount of contemporary precipitation alone is not an adequate index of the freshwater runoff from the land. The melting of snow in the drainage basins, resulting from the rising temperatures of April, may be a more important factor than the precipitation during that month.

To examine the possible effect of snow, snow data recorded at Goldstream Lake in March were compared with year-class abundance over a 15-year period (Fig. 19 and Appendix 19). Goldstream Lake on southern Vancouver Island was selected since it was the closest weather station to Barkley Sound that is at a sufficiently high altitude (1200 feet, 366 m) to receive an appreciable amount of snow. The snow data for the month of March were chosen on the basis that some snow or all of it would melt in late March and in April, and thereby increase

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[5] The seasonal weather of the British Columbia coast is generally determined by the position of the maritime polar air mass which moves in from the Pacific Ocean propelled by the pressure pattern (Johnston, 1952, 1953). In the summer this air mass follows a more northerly path than in winter. Since the air has not been subjected to as much heating from underneath (because of the more northerly path) it is not as unstable as in the winter. Consequently, northwesterly winds predominate in summer and precipitation is low. In the winter, moist warm unstable air approaches the coast from a general southwesterly direction after a long trajectory over warm Pacific waters giving precipitation as it is raised by the mountains. Also, prolonged spells of frontal weather result in long periods of southeasterly winds and heavy rain.

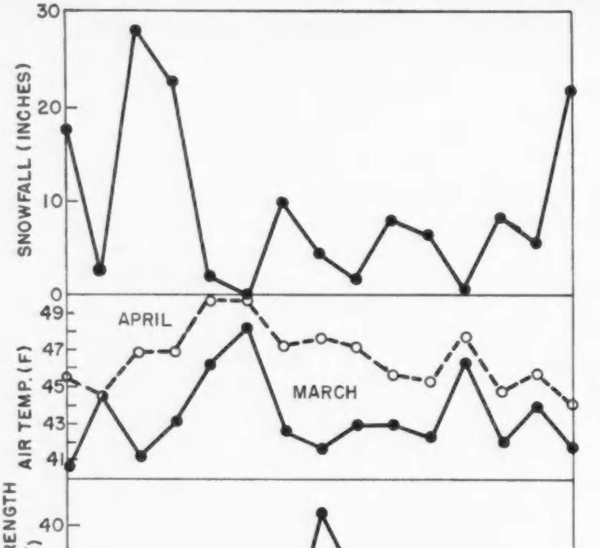

FIG. 19. March snowfall, March and April air temperature, and year-class strength on the lower west coast of Vancouver Island for the years 1936 to 1950. (Snowfall from Goldstream Lake; air temperature from Pachena Pt.; year-class data from Appendix 2.)

river discharge and the flow of currents in inshore areas during April, the main period of larval life.

An inverse relationship between snowfall and year-class strength can be readily detected for the data of most years. However, the data of two years, 1940 and 1941, show a striking departure from the general relationship. In these years, abnormally high temperatures prevailed (Fig. 19), and prevented snowfall on the drainage basin. Still, the year-classes of these years proved to be two of the poorest of the period. Lack of snow and little runoff should have been favorable to year-class survival.

The explanation of this apparent inconsistency, as well as of the lack of snow at the altitude of the weather station, may lie in the exceptionally high temperatures (the highest of the 15-year period). In spite of the high temperature, snow must have fallen at higher altitudes in March. Because of the increased temperature, snow probably melted at higher altitudes in April than would normally be melted at this time of year.

For one of the two years, 1941, discharge data at the Somass River are available. They show that in late March and early April the average flow was 4650 cubic feet per second (132 m^3/sec). This rate of flow was high in relation to that of other years for which data are available. In 1944 (which produced a relatively abundant year-class) the rate of flow was 2600 cubic feet per second (74 m^3/sec) or slightly over half as great as in 1941.

These data suggest that in 1941 (and probably also in 1940), river discharge and current flow were high. As a result, year-class strength would be reduced. Since precipitation in these years was relatively low, the heavy runoff would suggest extensive melting at high altitudes caused by greater than average air temperatures.

Delayed runoff, resulting from melting snow, appears to be a more critical factor than rain on river discharge and in herring survival.

Complexity of the Problem

While the relationship between snowfall and year-class abundance is of considerable interest and deserves further attention, it is too soon to affirm a causal connection. Other investigators have found such relationships involving air temperature, but the interpretation of these is questionable. Rounsefell (1930) obtained a statistically significant correlation between variation in average air temperature in the spring and variation in year-class abundance of herring in Alaska. Tester (1948), on the other hand, showed that an *inverse* correlation of equal significance could be obtained between air temperature in the spring and year-class strength of herring in British Columbia. A similar treatment applied to year-classes originating after those dealt with by Tester shows that no statistical relationship exists. · Poulsen (1936) and Jensen (1950) found inverse relationships between surface water temperature and numbers of herring larvae in the North Sea and in Danish waters; some of these relationships were apparently of statistical significance, but others were not.

Carruthers and Hodgson (1937), Carruthers (1951), and Carruthers *et al.*, (1951, 1953), have presented rather interesting data on the relationship between pressure gradients (and winds) and year-class abundance of Atlantic herring in European waters. The significance of their results has been questioned, however (Graham, 1952; Gulland, 1953).

Jensen (1927) and Kawana (1950) have suggested a possible relationship between number of sun spots and herring survival, but their supporting data are not convincing.

Numerous authors have speculated on the possible effect of food during the larval stage on herring survival, but with few exceptions (Soleim, 1942; Einarsson, 1952) the evidence for such a relationship is scant.

The results of herring research strongly suggest that hydrographic and related meteorological factors are intimately associated with the survival of herring, but that the relationship is probably a highly complicated one. It seems unlikely that any *single* meteorological factor will produce a simple index of future herring abundance.

SUMMARY

1. The central theme of this paper is that the vast mortality occurring during the larval stage in herring is traceable, at least insofar as the herring population of the lower west coast of Vancouver Island is concerned, to the transport of larvae by water currents from inshore waters to the open sea. It is maintained that a large proportion of the larvae, thus transported, do not survive.

2. This proposition was developed through studies, carried out from 1947 to 1951, on herring larvae mainly from Barkley Sound, British Columbia. Extensive sampling of the larval broods was undertaken throughout the period (March to May) that the planktonic larvae were present in the water. The sampling, which was mainly accomplished by towing nets horizontally through the water, was placed, on a quantitative basis as far as possible.

3. The herring of British Columbia spawn near shore in or just below the intertidal zone. Nearly three-quarters of the spawning on the lower west coast of Vancouver Island takes place along the northwest shore of Barkley Sound.

4. Study of the vertical distribution indicated that herring larvae were most highly concentrated near the surface of the water and during the night. As the larvae grew older, the preponderance of numbers in night samples as compared to daytime samples increased, and the preponderance of numbers in surface samples as compared to deep samples decreased.

5. The data suggested that the vertical distribution of larvae was influenced by intensity of light. Newly-hatched larvae appeared to be strongly attracted both to strong light (daylight) and to weak light (the faint light in surface waters at night). After absorption of the yolk sac, the attraction to strong light disappeared, and no heavy concentration of larvae was found in surface waters during the day. The fact that concentrations of larvae, comparable to those at the surface at night, were not found in the deep layers during the day, was attributed (a) to the greater ability of larvae to evade the sampling net during the day than at night, and (b) to the shallowness of the brood areas, which prevented the larvae from going sufficiently deep to reach the depth of preferred light intensity.

6. Study of the horizontal distribution showed heavy concentrations of larvae in the vicinity of the spawning grounds during the period that hatching was going on. After hatching ceased, the concentration of larvae in the inshore (or brood) areas progressively decreased at an approximately constant rate.

7. The extent of decrease of larvae noted in a brood area (Toquart Bay) appeared greater than would be expected on the basis of the average amount of larval mortality presumed to occur in the population. The fact that larvae were found in areas where no hatching had taken place indicated that a large part of the decrease was caused by movement of larvae away from the brood area.

8. The movement of larvae in the northern part of Barkley Sound (as shown by sampling) was interpreted on the basis of the pattern of water currents within the Sound (as determined by oceanographic survey). Large-scale movement of larvae took place along the northwest shore of the Sound (from the main

spawning grounds in and near Toquart Bay, to the mouth of the Sound); this movement of larvae was related to the strong seaward-moving current along the northwest shore. The seaward transport of larvae was hastened by the fact that rate of flow was greater in the surface layers where the larvae were found to be heavily concentrated at night. Low concentration of larvae in another part of the Sound was shown to result from the presence there of a compensatory current flowing from the open sea into the Sound.

9. These facts suggested that few of the larvae carried to sea were returned to the Sound. Moreover, they led to the contention that herring larvae, carried offshore, do not survive. While no direct evidence of the cause of death was available, several pieces of indirect evidence were put forward to support the contention. It was maintained that the strength of the year-class was derived from the larvae which remained in the Sound.

10. It was suggested that meteorological factors may affect year-class strength in herring through causing annual variations in rate of seaward flow of inshore currents during the critical larval period. The delayed effect of snowfall on river discharge was considered to be of greater importance than the more immediate effect of rainfall. It was obvious, however, that a number of interrelated meteorological factors (wind, rain, snow, and temperature) was operative. The conclusion was that no single meteorological factor was likely to provide a simple index for the survival of herring.

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APPENDIX 1. POPULATION ABUNDANCE AND FISHING MORTALITY ESTIMATES

As shown in Fig. 2, the catch on the west coast of Vancouver Island varied considerably in the period 1937–38 to 1953–54. These variations are considered to reflect population abundance, because (a) demand for herring during the period was consistently good and (b) fishing effort was generally high in all years except in 1945–46 (one of the years when catch was legally limited by quota—Tester, 1948) and in 1952–53 when no fishery occurred because of an industrial strike. For catch to indicate population abundance, the fishing mortality rate (i.e., the ratio of the number of fish caught to the total number present in the population at the beginning of the season) must have remained constant during the period. Fishing mortality rates, as calculated by Stevenson and Outram (1953), were reasonably constant, varying from 0.59 to 0.69 (Table A), which explains the similarity in the fluctuations of population abundance and catch from 1946–47 to 1952–53 (Fig. 2). Population abundance for years earlier than 1946–47 are not calculated since data on spawning deposition for earlier years are not considered sufficiently accurate.

TABLE A. Estimated population abundance and fishing mortality of the herring stocks of the lower west coast of Vancouver Island in the fishing seasons 1946–47 to 1952–53.

Fishing season	No. of fish in catch C	No. of spawning fish S	Population abundance P = C + S	Fishing mortality rate C/P
	millions	*millions*	*millions*	
1946–47	330	170	500	0.66
1947–48	230	140	370	0.62
1948–49	210	140	350	0.60
1949–50	290	130	420	0.69
1950–51	160	110	270	0.59
1951–52	110	60	170	0.65
1952–53	0	130	130	0
Geometric mean (excluding 1952–53)				0.63

APPENDIX 2. STRENGTH OF HERRING YEAR-CLASSES

Four steps were involved in determining relative year-class abundance on the lower west coast of Vancouver Island. Age composition data and average weight of fish at each age (Table B) permit determination of the average weight of all fish in each year's catch. In Table C the number of fish in the catch is estimated as equal to the weight landed divided by the estimated average weight of an individual fish in each year. In Table D the number of fish caught is divided among the various ages in proportion to their representation in the samples.

Finally, year-class strength is obtained by summing the numbers of fish contributed to the catch by a particular year-class in successive years.

The 1936 year-class, for example, contributed 10 million fish at Age II (more accurately, as they neared Age II in late 1937 and early 1938), 24 at Age III, 11 at Age IV, 16 at Age V, 2 at Age VI, and 1 at Age VII, making a total contribution of 64 million fish. The contributions of other year-classes have been similarly calculated, with the result that the relative abundance of the various year-classes is as follows, in millions:

1936 — 64
1937 — 142
1938 — 82
1939 — 46
1940 — 26
1941 — 61
1942 — 115
1943 — 429
1944 — 263
1945 — 235
1946 — 198
1947 — 307
1948 — 102
1949 — 128
1950 — 135

For the 1949 and 1950 year-classes above, it was assumed that 1 million fish would be contributed by the 1949 year-class as VI-year fish in the 1954-55 fishery and that 15 million fish would be contributed by the 1950 year-class as V-year and VI-year fish in the 1954-55 and 1955-56 fisheries. Contributions of this order have been made by previous year-classes as V-year and VI-year fish (Table D).

The figures above are plotted in Fig. 3.

TABLE B. Age composition by season, and average weight of a herring at each "age" (year of life), in grams, over the seasons 1937–38 to 1953–54.

Fishing season	Percentage "age" composition								
	I	II	III	IV	V	VI	VII	VIII	IX+
1937–38	0.0	7.0	60.2	18.3	10.9	1.8	1.2	0.4	0.2
1938–39	0.0	53.2	30.0	13.3	2.0	1.3	0.2	0.0	0.0
1939–40	0.0	18.2	59.1	15.4	5.5	1.0	0.7	0.0	0.1
1940–41	0.0	4.0	40.2	38.7	12.9	3.4	0.5	0.2	0.1
1941–42	0.0	1.9	40.1	24.4	25.3	6.4	1.3	0.5	0.1
1942–43	0.0	1.8	24.6	39.3	21.0	8.6	3.5	1.2	0.0
1943–44	0.0	15.7	44.2	17.3	15.3	5.7	1.6	0.1	0.1
1944–45	10.7	40.8	33.9	8.7	1.6	2.5	1.5	0.1	0.2
1945–46	0.0	10.4	76.0	9.7	2.2	0.6	0.9	0.1	+
1946–47	+	6.2	45.5	38.9	6.8	2.0	0.4	0.1	+
1947–48	+	3.6	61.6	25.0	8.0	1.4	0.2	0.1	+
1948–49	0.1	15.0	54.4	25.6	3.6	1.1	0.2	+	0.0
1949–50	+	4.6	67.3	21.6	5.5	0.7	0.2	0.1	0.0
1950–51	+	9.4	39.5	42.6	6.7	1.4	0.3	+	+
1951–52	0.1	5.3	66.1	19.8	7.9	0.8	0.1	0.0	0.0
1952–53	0.1	7.8	56.5	33.2	1.9	0.6	0.0	0.0	0.0
1953–54	+	2.9	62.6	27.7	5.9	0.5	0.2	0.1	+
Weight (g)	20	60	90	114	130	145	155	160	165

TABLE C. Total catch, average weight of fish in catch and number of fish in catch.

Fishing season	Total catch	Average wt. of fish	No. of fish in catch
	10^8*g*	*g*	*millions*
1937–38	139	98.85	141
1938–39	63	78.87	80
1939–40	63	91.87	70
1940–41	130	105.66	123
1941–42	31	110.20	28
1942–43	32	115.13	28
1943–44	82	99.87	82
1944–45	109	75.56	144
1945–46	263	91.08	289
1946–47	335	101.64	330
1947–48	230	99.10	232
1948–49	198	93.75	211
1949–50	283	96.59	293
1950–51	165	101.05	163
1951–52	107	96.75	111
1952–53	66[a]	96.64	68[a]
1953–54	269	98.62	273

[a]Estimated on the basis of what the catch would have been if the fishing mortality had equalled the average of the 1946–47 to 1951–52 period (See Appendix 1). No fishing occurred in 1952–53.

TABLE D. Number of fish of each age in the herring catch of the lower west coast of Vancouver Island, in millions.

Fishing season	Total catch	Number of fish at each age								
		I	II	III	IV	V	VI	VII	VIII	IX+
1937–38	141	0	10	85	26	15	2	2	1	+
1938–39	80	0	43	24	11	2	1	+	0	0
1939–40	70	0	13	41	11	4	1	+	0	1
1940–41	123	0	5	49	48	16	4	1	+	+
1941–42	28	0	+	11	7	7	2	+	+	+
1942–43	28	0	+	7	11	6	2	1	+	0
1943–44	82	0	13	36	14	12	5	1	+	+
1944–45	144	15	59	49	12	2	4	2	+	+
1945–46	289	0	30	220	28	6	2	3	+	+
1946–47	330	+	20	150	128	22	7	1	+	+
1947–48	232	+	8	143	58	19	3	+	+	+
1948–49	211	+	32	115	54	8	2	+	+	0
1949–50	293	+	14	197	63	16	2	1	+	0
1950–51	163	+	15	64	69	11	2	+	+	+
1951–52	111	+	6	73	22	9	1	+	0	0
1952–53	68[a]	+	5	38	23	1	+	0	0	0
1953–54	273	+	8	171	76	16	1	+	+	+

[a]See footnote to Table C.

APPENDIX 3.

TABLE E. Number of samples of herring larvae taken on the west coast of Vancouver Island from 1947 to 1951, according to general locality and depth of sampling, and time of day.

Depth (*fathoms*)	Lower west coast of Vancouver Island						Upper west coast of Vancouver Island		Totals
	Barkley Sd. (Southern part)		Barkley Sd. (Northern part)		Clayoquot Sd. and Sydney In.				
	Day	Night	Day	Night	Day	Night	Day	Night	
1947									
0 -0.5	6	16	13	20	0	10	0	14	79
0.6-1.0	0	0	1	0	1	3	0	0	5
1.1-2.0	0	3	3	8	3	6	0	3	26
2.1-3.0	2	5	6	4	0	29	0	5	51
3.1-4.0	1	3	3	6	2	19	0	4	38
4.1-5.0	4	2	6	6	1	7	0	4	30
5.1-6.0	2	5	4	5	1	3	0	1	21
6.1-7.0	1	1	2	1	1	0	0	0	6
7.1-8.0	1	0	2	2	1	0	0	0	6
8.1-9.0	0	1	0	1	0	0	0	0	2
9.1-10.0	1	0	1	0	1	1	1	0	5
10.1-11.0	0	0	3	1	0	0	0	0	4
11.1-12.0	0	0	2	0	1	0	0	0	3
12.1-13.0	1	0	0	0	0	0	0	0	1
15.1-16.0	1	0	0	0	0	0	0	0	1
40.1-50.0	1	0	0	0	0	0	0	0	1
Totals	21	36	46	54	12	78	1	31	279
1948									
0 -0.5	9	17	18	37	35	50	54	147	367
0.6-1.0	0	0	1	8	2	9	4	6	30
1.1-2.0	0	2	1	8	1	7	14	34	67
2.1-3.0	2	6	4	11	13	16	18	33	103
3.1-4.0	5	1	4	15	2	11	9	20	67
4.1-5.0	1	4	0	4	1	3	3	14	30
5.1-6.0	1	0	1	2	2	0	1	7	14
6.1-7.0	0	1	0	3	0	6	1	4	15
7.1-8.0	0	0	0	0	0	0	0	4	4
8.1-9.0	0	0	0	0	0	1	0	0	1
11.1-12.0	0	0	0	0	0	0	0	1	1
Totals	18	31	29	88	56	103	104	270	699

TABLE E—Continued

Depth (*fathoms*)	Lower west coast of Vancouver Island						Upper west coast of Vancouver Island		Totals
	Barkley Sd. (Southern part)		Barkley Sd. (Northern part)		Clayoquot Sd. and Sydney In.				
	Day	Night	Day	Night	Day	Night	Day	Night	
1949									
0 –0.5	0	5	20	74	27	69	99	191	485
0.6–1.0	0	0	2	5	4	7	31	32	81
1.1–2.0	0	3	4	35	2	17	30	84	175
2.1–3.0	0	0	0	6	0	16	19	44	85
3.1–4.0	0	0	0	8	1	5	13	31	58
4.1–5.0	0	0	0	6	0	2	5	6	19
5.1–6.0	0	0	0	4	0	4	0	2	10
6.1–7.0	0	0	0	1	0	0	0	0	1
Totals	0	8	26	139	34	120	197	390	914
1950									
0 –0.5	0	0	106	433	5	94	7	133	778
0.6–1.0	0	0	1	9	0	0	0	0	10
1.1–2.0	0	0	7	27	0	0	0	0	34
2.1–3.0	0	0	96	206	1	16	0	11	330
3.1–4.0	0	0	89	178	0	17	4	26	314
4.1–5.0	0	0	16	20	3	37	2	53	131
5.1–6.0	0	0	1	4	0	19	0	16	40
6.1–7.0	0	0	2	1	0	0	1	0	4
7.1–8.0	0	0	0	2	0	0	0	0	2
Totals	0	0	318	880	9	183	14	239	1643
1951									
0 –0.5	0	0	87	249	0	0	0	0	336
0.6–1.0	0	0	0	5	0	0	0	0	5
1.1–2.0	0	0	1	7	0	0	0	0	8
2.1–3.0	0	0	4	4	0	0	0	0	8
3.1–4.0	0	0	41	37	0	0	0	0	78
4.1–5.0	0	0	0	1	0	0	0	0	1
5.1–6.0	0	0	0	2	0	0	0	0	2
Totals	0	0	133	305	0	0	0	0	438
Grand Total	39	75	552	1466	111	484	316	930	3973

APPENDIX 4. NETS USED TO CAPTURE HERRING LARVAE

Table F gives details of nets used and their theoretical straining capacity at the average towing speeds used in various years. The Hensen net is that described by Hensen (1887). The metal net used in 1948 has been described by Tester and Stevenson (1948). Clarke and Bumpus described their well-known sampler in 1940.

The "straining capacity" shown in the last column of Table F is the (theoretical) quantity of water which would pass through the net, when towed at the average speed shown, if it were to offer no resistance at all to the passage of water through it.

TABLE F. Specifications of various nets used to capture herring larvae. 1 inch = 2.54 cm; 1 square inch = 6.45 cm²; 1 knot = 1.855 km/hour; 1 Imperial gallon per minute = 4.546 litre/min.

Type of net	Design	Year used	No. of meshes per inch	Diameter of net mouth	Greatest diam. of straining portion	Length of straining portion	Area of straining surface	Average towing speed	"Straining capacity"
				inches	*inches*	*inches*	*sq. in.*	*knots*	*gal/min*
Cotton	Conical	1947	29	30	30	72	3470	1.5	4650
Silk	Conical	1948	38	24	24	72	2750	1.5	2980
Silk	Hensen	1949	29	18	24	72	2750	2.5	2790
		1950	29	18	24	72	2750	1.8	2010
		1951	29	18	24	72	2750	1.2	1340
Metal	Tester & Stevenson	1948	30	6	12	48	1620	9.0	1120
Plankton sampler	Clarke and Bumpus	1949	29	4.9	4.9	24	184	2.5	205
		1950	29	4.9	4.9	24	184	1.8	148
		1951	29	4.9	4.9	24	184	1.2	100

APPENDIX 5. THE FRACTIONAL METHOD OF ESTIMATING NUMBERS OF LARVAE IN A SAMPLE

DETAILS OF THE METHOD

The sample (or sub-sample, when extremely large numbers of larvae were collected) was poured into a shallow, rectangular, glass dish, 10 by 6 inches by 1½ inches deep (25×15×3.8 cm). On the bottom of the dish, a grid was marked off into 60 squares, each of which was 1 square inch (645 mm² in area). (Alternately, a similar grid was outlined on a painted wooden board, and the board was suitably positioned under the counting dish.) The contents were stirred until it appeared that the larvae were spread evenly over the bottom of the dish. Then accurate counts were made of the larvae overlaying 10 predesignated, widely-scattered grid squares (i.e., ⅙ of the area of the plate). When more than half the length of a larva was included in a particular square it was considered as being within that square, but when less than half of its length was contained in the square it was excluded from the count.

STATISTICAL TEST OF THE ACCURACY OF THE METHOD

An experiment was carried out to test the validity of this method of estimating the number of larvae in large samples. The experiment was designed (1) to determine whether the larvae were evenly distributed over the selected squares in which counts were made, or whether there was a tendency for larvae to be concentrated in certain areas of the glass dish, and (2) to ascertain if significantly different counts would be expected if one person worked over the same sample twice. In this experiment, a large sample was divided into 5 sub-samples and the numbers of larvae overlaying the 10 predesignated squares were counted for each sub-sample. Then the procedure was repeated with the larvae in each sub-sample being redistributed in the dish.

The results of this experiment are shown in Table G. The analysis of variance is as follows:

Source of variability	Sum of squares	Degrees of freedom	Variance
Total	5501.0	99	
Between sub-samples	2351.0	4	587.8
Between squares	466.1	9	51.8
Between counts	114.5	1	114.5
Error component	2569.4	85	30.2

F (counts of individual squares) = 1.72 : $F_{.05}$ = 1.99
F (first and second count) = 3.80 : $F_{.05}$ = 3.96
F (sub-samples) = 19.59** : $F_{.01}$ = 3.56

The significant difference between counts of sub-samples was expected, since no effort was made to divide the contents of the sample into equal-sized sub-samples.

The actual number of the larvae in the total sample amounted to 4887. The total number, calculated by assuming that the combined counts of the sub-samples represented ⅙ of the total number of larvae in the sample, differed from the actual count by 8.4% in the case of the first fractional count and by 4.7% on the basis of the second count.

TABLE G. Results obtained when a fraction of a sample of larvae was enumerated in two separate counts by the same person (in each count the sample was divided into 5 sub-samples).

Sub-sample	Count	Grid squares selected for counting										Total
		A	B	C	D	E	F	G	H	I	J	
1	1	13	24	8	23	16	16	15	10	9	6	140
	2	12	8	16	9	9	6	16	10	14	16	116
2	1	19	28	13	17	9	13	15	10	11	19	154
	2	5	22	8	26	11	24	20	23	25	16	180
3	1	26	30	19	22	28	18	14	28	20	3	208
	2	36	15	34	27	25	37	18	14	20	21	247
4	1	17	14	19	23	23	21	19	12	0	19	167
	2	22	24	33	22	6	27	27	23	14	14	212
5	1	2	8	12	10	17	1	9	3	9	6	77
	2	11	17	17	11	8	3	8	9	9	5	98
Total	1	77	104	71	95	93	69	72	63	49	53	746
	2	86	86	108	95	59	97	89	79	82	72	853

STATISTICAL TEST OF THE DIFFERENCES OBTAINED BY DIFFERENT PERSONS COUNTING THE SAME SAMPLE

Three persons made fractional counts of the larvae in the same sample. The larvae were re-distributed over the grid squares after each person counted. Results are in Table H, and the analysis is as follows:

	Sum of squares	Degrees of freedom	Variance
Total	1194	29	
Between samplers	3.6	2	1.8
Between counts of squares	407.0	9	45.2
Error component	783.4	18	43.5

F (between samplers) — not significant (variance less than that of error component)
F (between counts of squares) = 1.04 : $F_{.05}$ = 2.46

In addition to showing no significant difference between the counts of the samplers, the experiment corroborated the results of the previous experiment (Table G) in showing no significant difference between the individual counts of larvae overlying the grid squares.

The calculated number of larvae in the sample, derived by multiplying each of the samplers' fractional counts by 6, varied from the actual count of the whole sample (1080) by 2.2, 3.3, and 1.1% respectively.

TABLE H. Counts of larvae made by three samplers on a fraction (1/6) of the same sample.

Samplers	Grid squares selected for counting										Total
	A	B	C	D	E	F	G	H	I	J	
1	15	28	17	10	23	19	11	21	23	9	176
2	8	19	18	12	18	29	14	25	13	18	174
3	8	23	18	28	25	11	28	15	12	14	182
Totals	31	70	53	50	66	59	53	61	48	41	532

APPENDIX 6. CONSISTENCY OF THE PROCEDURE FOR MEASURING HERRING LARVAE

In Table J details are given of two experiments in which each of 5 persons measured the same group of larvae. Deviations of each frequency from the average (in the last column) are squared and divided by the average; their sum is the χ^2 figure shown. The P-value is the probability of the observed deviation of each worker's measurements from the average occurring by chance.

TABLE J. Results of two experiments in each of which five persons independently measured the same group of larvae.

Length class (*mm*)	**Experiment 1** Distributions of measurements by different workers					Averaged distribution
	A	B	C	D	E	
7	1	0	0	2	3	1.2
8	17	12	13	8	11	12.2
9	5	9	4	10	7	7.0
10	9	5	9	8	6	7.4
11	13	20	25	13	28	19.8
12	38	32	35	29	33	33.4
13	22	26	22	28	21	23.8
14	10	9	7	14	6	9.2
15	5	7	5	8	5	6.0
Totals	120	120	120	120	120	120.0
χ^2	5.85	1.93	3.94	9.03	5.30	...
P-value	0.45	>0.90	0.65	0.15	0.50	...
			Experiment 2			
15	1	1	1	1	0	0.8
16	2	2	4	2	2	2.4
17	16	15	15	15	18	15.8
18	45	45	43	36	38	41.4
19	43	43	41	44	43	42.8
20	10	13	15	19	16	15.0
21	1	1	1	2	3	1.6
22	0	0	0	1	0	0.2
Totals	120	120	120	120	120	120.0
χ^2	1.17	0.83	0.23	2.54	0.62	...
P-value	0.55	0.65	0.90	0.27	0.75	...

APPENDIX 7. METHODS OF DETERMINING THE STRAINING CAPACITY OF GEAR USED IN THE VARIOUS SAMPLING METHODS

The straining capacity of the gear used in each method of sampling was determined in order to convert the actual number of larvae taken in each sample to the number that would have been taken if a standard volume (10,000 Imperial gallons or 45,500 litres) of water had been strained. The general formula developed for this purpose was:

$$\frac{10{,}000\,n}{t\,g}$$

where n is the actual number of larvae in the sample, t the duration of sampling in minutes, and g the straining capacity in gallons per minute.

Straining Capacity of the Pump

The amount of water strained per minute in the course of sampling with a pump was readily determined. From time to time during the two years that the method was used (1948 and 1949), accurate determinations were made of the time necessary to fill a barrel of known volume. The average number of gallons pumped per minute was 100, with individual tests varying from 92 to 104 (Table K). The formula for standardizing pump samples was, therefore:

$$\frac{10{,}000\,n}{100\,t}, \text{ or } \frac{100\,n}{t}$$

Table K. Determinations of the amount of water strained in sampling by pumping. (1 gal. = 4.55 l.)

Date	Capacity of barrel	Time to fill barrel	Straining capacity of the method
	gal.	*min.*	*gal/min.*
April 8, 1948	39.5	0.435	93
April 9, 1948	39.5	0.405	98
April 13, 1948	39.5	0.380	104
April 14, 1948	39.5	0.380	104
May 3, 1948	36.0	0.354	102
May 3, 1948	34.0	0.342	99
April 9, 1949	38.0	0.385	99
April 9, 1949	37.0	0.400	92
April 17, 1949	38.0	0.365	104
April 18, 1949	37.0	0.365	101
Average			100

Straining Capacity of Clarke-Bumpus Plankton Samplers

Clarke-Bumpus plankton samplers were designed to provide investigators with information on the amount of water strained. They are equipped with a counter which is activated by a propellor turning at a rate proportional to the volume of water strained through the net. The inventors of the sampler have determined that 1 unit recorded on the counter is equivalent to 4 litres or 0.88 Imperial gallon of water strained (D. F. Bumpus, personal communication). This relationship is considered to be maintained over a relatively wide range of towing speeds (Clarke *et al.*, 1943). Hence, if u represents the number of counter units recorded during a tow, $0.88\,u$ will be the number of gallons of water strained, and $0.88u/t$ will be the number of gallons per minute, or the straining capacity, g. Knowing g, the formula for standardizing samples taken with the plankton samplers can be determined from the general formula:

$$\frac{10{,}000\,n}{t\,g} = \frac{10{,}000\,n}{t\,\dfrac{0.88u}{t}} = \frac{11{,}360\,n}{u}$$

Since the same plankton sampler was not used throughout the investigation, experimental tows were made over measured distances to compare the number of units recorded per minute by the different samplers at various speeds of tow. The results, shown in Fig. 20, indicate that at any given speed of tow the number of counter units per minute on the 1949 and 1951 plankton samplers was about 1.63 times as great as the number recorded by the 1950 plankton sampler. Since the specifications in the manufacture of each sampler were identical, a difference in the amount of friction in the counter mechanism seemed a plausible explanation for the observed discrepancy in operation. In personal correspondence Dr D. F. Bumpus has confirmed this view, stating that a relatively small amount of friction has been shown to alter counter readings greatly.

The above formula, 11,360 n/u, therefore, could be applied only to samples taken by the 1949 and 1951 plankton samplers. While these samplers presumably had the same straining capacity as the 1950 sampler, the number of counter units of the former samplers was 1.63 times that of the latter. Therefore, the formula for samples taken with the 1950 sampler was:

$$\frac{11{,}360\ n}{1.63\ u} = \frac{6970\ n}{u}$$

STRAINING CAPACITY OF SILK NETS USED IN 1949, 1950, AND 1951

The silk nets used in the last 3 years of the investigation were all of Hensen egg-net design and with the same diameter of opening. Their straining capacity was determined by comparison with the known straining capacity of Clarke-Bumpus samplers. The comparison was accom-

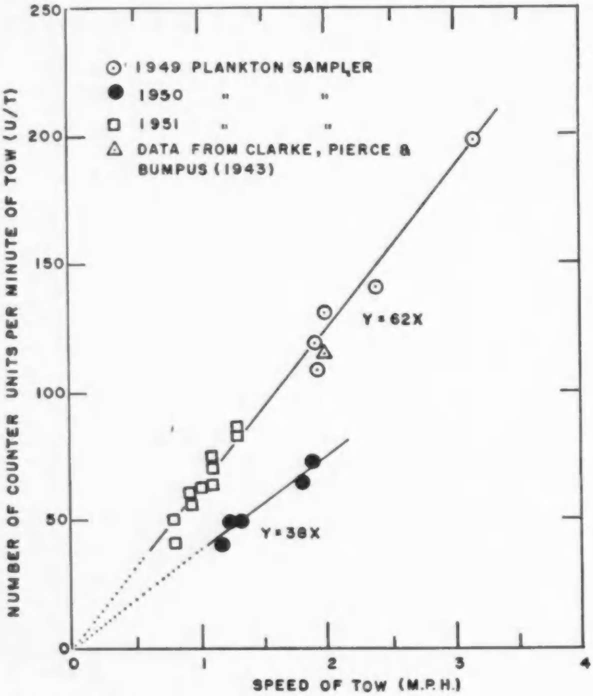

FIG. 20. Number of counter units recorded per minute by the Clarke-Bumpus plankton samplers used in 1949, 1950 and 1951, in relation to speed of tow.

TABLE L. Numbers of larvae taken by Clarke-Bumpus plankton samplers (a), and by silk nets (b), in simultaneous tows in 1949 and 1950. Four different towing speeds were used, their geometric means being 1.0, 1.6, 3.1 and 3.9 knots (1.9, 3.0, 5.8 and 7.2 km/hr.)

Speed (*knots*)	Number of larvae a	Number of larvae b	Ratios a/b
1950			
1.0	3	47	0.064
1.0	3	65	0.046
1.0	1	42	0.024
1.0	8	105	0.076
0.9	4	90	0.044
0.9	12	136	0.087
1.0 (GM)			0.052*
1949			
1.8	17	245	0.070
1.8	5	97	0.052
1.5	423	7029	0.060
1.7	1310	17,008	0.077
1.4	1195	13,669	0.087
1.9	38	386	0.098
1.3	23	681	0.034
1.7	104	6670	0.016
1.6 (GM)			0.055*
1949			
3.1	200	4340	0.046
3.1	271	3065	0.088
3.2	4	34	0.118
3.2	18	190	0.095
3.2	7	71	0.099
2.9	182	1110	0.164
3.1 (GM)			0.095*
1949			
3.5	157	1185	0.132
3.5	1040	8163	0.128
3.5	5	45	0.111
4.5	15	84	0.179
3.9	15	98	0.153
4.4	20	134	0.149
3.9 (GM)			0.140*

Comparison of mean ratios (*) at different speeds of tow.

(1) Mean ratios at average towing speeds of 1.0 and 1.6 knots: $t = 0.40$, $P = 0.70$ (not significant).

(2) Mean ratios at average towing speeds of 1.6 and 3.1 knots: $t = 2.69$, $P = 0.02$ (significant).

(3) Mean ratios at average towing speeds of 3.1 and 3.9 knots: $t = 2.21$, $P = 0.05$ (significant).

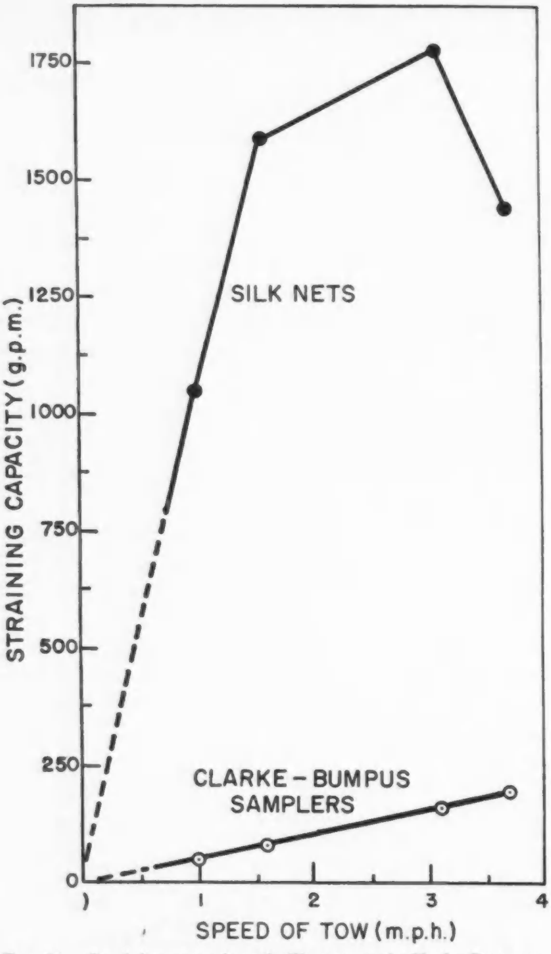

FIG. 21. Straining capacity of silk nets and Clarke-Bumpus plankton samplers in relation to speed of tow. (m.p.h. = knots = nautical miles per hour.)

plished by towing simultaneously a plankton sampler with a silk net, taking necessary precautions to ensure with reasonable certainty that both types of gear passed through the same concentration of larvae. Insofar as possible, the two types of gear were towed at the same depth, at the same time, in the same place, and from the same towing boat.

The results (Table L) showed that at slow speeds of tow, 1.0 and 1.6 knots (1.9 and 3.0 km/hr) the straining capacity of Clarke-Bumpus samplers was about 5% that of the silk nets. At 3.1 knots (5.8 km/hr) the straining capacity of the former was 10% of the latter, and at 3.9 knots (7.2 km/hr) it was 14%. (General scrutiny of the mean ratios suggests that these calculated for 1.0 and 1.6 knots are not significantly different, but that there are significant differences between these and those for 3.1 and 3.9 knots. The t-test of significance confirms these indications—see Table L.)

The straining capacity of the Clarke-Bumpus samplers, in gallons per minute, can be calculated for the 4 speeds at which the simultaneous hauls were taken (1) by formulae given previously (page 797), and (2) from values of u/t given in Fig. 20. The computed straining capacity of the plankton samplers at the 4 speeds of tow are plotted in Fig. 21 together with the straining capacity of the silk nets calculated from the ratios in Table L. The speed at which the silk nets were towed (necessary information for determining their straining capacity) was estimated by means of metre readings of Clarke-Bumpus samplers towed simultaneously. The metre readings could be converted directly to speed of tow using Fig. 20.

It is of interest to note (Fig. 21) that while the straining capacity of the silk nets increased with increasing speed of tow up to 1.6 knots (apparently in almost linear fashion), it levelled off at higher speeds and showed a distinct decrease when a speed of 3.7 knots was reached. Apparently at a towing speed of about 3 knots a critical point is reached beyond which the decrease in net efficiency (the ratio of straining capacity to the theoretical maximum straining capacity) overtook the increase in the amount of water through which the net passed in unit time.

STRAINING CAPACITY OF SILK NETS USED IN 1948

The straining capacity of the conical silk nets used in 1948 was calibrated by means of the pump which was also employed in sampling that year (Clarke-Bumpus plankton samplers were not obtained until 1949). The numbers of larvae taken by the silk nets were compared with the numbers taken by pumping at approximately the same time, place and depth of sample (Table M). The speed of tow of the silk nets was kept as constant as possible (1.5 knots).

TABLE M. Ratio of number of larvae taken by silk net and pump in 1948.

No. of larvae taken per minute		Ratio
Pump	Silk net	
2.1	23.5	0.090
17.9	629.0	0.028
7.5	167.0	0.045
0.3	2.9	0.103
Mean (GM)		0.058

The results suggested that the straining capacity of the pump was about 6% that of the silk net. Since the pump strained 100 gallons of water per minute, the silk net therefore strained about 1700 gal/min (7700 l/min) at the towing speed of 1.5 knots (2.8 km/hr). This straining capacity did not differ greatly from that of nets of Hensen egg-net design (Fig. 21) at a comparable speed of tow. However, the theoretical straining capacity of the 1948 silk nets was 1.8 times as great as that of the Hensen nets (Appendix 4), showing the much lower straining efficiency of the former. The low efficiency was probably a result of the finer mesh used (38, as against 29, meshes per inch) and the difference in design.

The lack of simultaneous tows with plankton samplers in 1948 prevented accurate assessment of speeds of towing. A general indication of speed of towing was obtained from timing the speed of the towing boat over measured distances. It was found that the average speed was about 1.5 knots and that speeds ranged between 1 and 2 knots.

In view of the lack of precise data on speed, the calculated straining capacity of 1700 gal/min was used for all silk net hauls in 1948, giving a formula for standardization of:

$$\frac{10{,}000\,n}{1700\,t},\ \text{or}\ \frac{5.9\,n}{t}$$

STRAINING CAPACITY OF THE COTTON NET USED IN 1947

No method was available for calibrating the tows taken with a conical-shaped cotton net in the preliminary survey of 1947. A rough standardization of the samples was attempted by considering the net as 50% efficient in all hauls, regardless of speed of tow (speed of tow varied from 1 to 2 knots). In other words, it was assumed that the straining capacity was half of the theoretical straining capacity of 4650 gal/min at 1.5 knots (Appendix 4). The formula for standardizing the samples, therefore, became:

$$\frac{10{,}000\,n}{\frac{1}{2}(4650)t},\ \text{or}\ \frac{4.3\,n}{t}$$

STRAINING CAPACITY OF THE METAL NET USED IN 1948

As the in case of the cotton nets used in 1947, the straining capacity of the metal nets could not be experimentally determined, and the assumption of 50% efficiency was likewise adopted. Since its theoretical straining capacity was 1120 gal/min at 9 knots, the formula for treating the samples was:

$$\frac{10{,}000\,n}{\frac{1}{2}(1120)t},\ \text{or}\ \frac{18\,n}{t}$$

The metal nets were always towed from the seine boat, and the speed of the vessel varied little from 9 knots.

APPENDIX 8. NUMBER AND SIZE OF LARVAE CAPTURED AT DIFFERENT DEPTHS

Table N summarizes the variations in number of larvae taken with depth, at several places and times, grouped into three size ranges.

TABLE N. Average number of larvae per sample, and average length of larvae in millimetres, at different depths at three stages of development.

Depth	Recently-hatched larvae (day and night samples combined)					
	Queen Cove, Mar. 26-Apr. 5, 1949			Toquart Bay, Apr. 1-5, 1950		
(*fathoms*)	No. of samples	No. of larvae	Length (*mm*)	No. of samples	Av. no. of larvae	Length (*mm*)
0 -0.5	9	22,480	8.7	5	1,150	8.7
0.6-1.0	5	7,340	8.8	..	..	..
1.1-2.0	5	5,010	8.9	..	..	..
2.1-3.0	6	4,580	9.0	3	570	8.6
3.1-4.0	3	4,000	9.3	3	325	9.1
4.1-5.0	2	3,100	8.6	1	300	9.1
	Larvae of intermediate length (night samples only)					
	Queen Cove, Apr. 21-25, 1949			Toquart Bay, May 1-10, 1950		
0 -0.5	4	530	12.0	2	17.3	13.4
0.6-1.0	4	940	12.2	..	..	..
1.1-2.0	4	224	14.2	..	..	..
2.1-3.0	1	164	15.1	2	5.2	13.8
3.1-4.0	1	162	15.8	1	0.7	15.0
4.1-5.0	1	164	14.3	2	1.7	14.5
	Larvae approaching metamorphosis (night samples only)					
	Whitepine Cove, May 18-20, 1947			Nuchatlitz Inlet, May 13-14, 1947		
0 -1.5	3	31.7	21.3	5	68.8	20.2
1.6-4.0	22	152.2	22.8	3	8.3	24.5
4.1-6.0	6	54.5	22.5	2	22.0	19.9

APPENDIX 9. COMPARISON OF LENGTHS OF HERRING LARVAE NEAR THE SURFACE AND AT GREATER DEPTHS

Samples of larvae were taken at night in Queen Cove April 21–25, 1949, above and below a depth of 1 fathom (1.8 m). Length frequency distributions are shown in Table O. The larvae from deeper water averaged 2.81 mm longer, a highly significant difference ($t = 14.4; t_{.001} = 3.29$; $P<0.001$).

TABLE O. Length frequency of herring larvae from Queen Cove, taken above and below a depth of 1 fathom (1.8 m).

Length	Above depth of one fathom		Below depth of one fathom	
mm	*no.*	%	*no.*	%
7	17	3.5	1	0.3
8	79	15.1	8	2.4
9	62	11.8	9	2.7
10	39	7.4	8	2.4
11	42	8.0	2	0.6
12	26	5.0	7	2.1
13	41	7.8	24	7.0
14	55	10.5	47	13.9
15	79	15.1	82	24.3
16	59	11.3	77	22.7
17	18	3.4	53	15.7
18	6	1.1	18	5.3
19	..	..	1	0.3
20	..	..	1	0.3
Totals	523	100.0	338	100.0
Av. length	12.08 mm		14.89 mm	
Sum of squares	5023		1706	

APPENDIX 10. DIURNAL VARIATION IN NUMBER AND SIZE OF HERRING LARVAE CAPTURED

Table P shows two series of samples taken over a 24-hour period. In general, the larvae taken at night were far more numerous and averaged slightly larger than those taken by day. The transition from day to night conditions was quite sharp. For example, of the 4 samples taken above 1 fathom in Queen Cove at 19:30–22:30 hours, two were taken at dusk and two after dusk. In the former, the average number of larvae was 370 and the average length 9.4 mm; in the latter, the average number of larvae was 4150 and the average length 12.8 mm.

TABLE P. Samples taken over a 24-hour period, grouped by 3-hour intervals, showing average number of larvae per sample and average length of larvae.

Time of sampling (*hours*)	0–1 fathom (0–1.8m)			2–4 fathoms (3.7–7.3m)		
	No. of samples	No. of larvae	Length (*mm*)	No. of samples	No. of larvae	Length (*mm*)
			QUEEN COVE, APRIL 20–21, 1949.			
07:30–10:30	3	35	12.0	4	52	10.3
10:30–13:30	2	38	10.4	..	..	..
13:30–16:30	2	74	12.2	..	..	..
16:30–19:30	4	24	10.5	..	..	..
19:30–22:30	4	2,260	12.5	3	793	11.4
22:30–01:30	2	2,100	12.6	..	..	..
01:30–04:30	3	1,310	12.7	..	..	..
04:30–07:30	2	18	11.0	..	..	..
			TOQUART BAY, APRIL 8–9, 1950.			
07:30–10:30	4	620	9.1	4	69	9.3
10:30–13:30	2	1,750	9.3	1	116	9.2
13:30–16:30	2	1,720	8.6	2	38	9.2
16:30–19:30	3	2,200	8.9	4	137	9.7
19:30–22:30	3	13,000	10.5	3	412	10.5
22:30–01:30	3	12,600	10.8	3	753	10.3
01:30–04:30	4	18,000	9.5	4	468	9.8
04:30–07:30	2	370	9.0	2	76	9.4

APPENDIX 11. LENGTHS OF HERRING LARVAE IN DAY AND NIGHT SAMPLES

Table Q compares length frequencies of larvae in day and night samples from Toquart Bay, taken April 8–9, 1950. The boundary between day and night was taken as 04:30 and 19:30 hours. The difference of 1.12 mm between the two series is highly significant ($t = 17.0; t_{.001} = 3.29$).

TABLE Q. Length frequency distributions of herring larvae taken by day and by night, Toquart Bay, April 8-9, 1950.

Length	Daytime		Night	
mm	*no.*	%	*no.*	%
6	8	0.9	8	0.8
7	105	11.7	39	3.8
8	220	24.5	120	11.7
9	277	31.0	199	19.6
10	203	22.6	283	27.6
11	64	7.1	206	20.1
12	14	1.6	103	10.0
13	6	0.7	45	4.4
14	..	..	14	1.4
15	..	..	7	0.7
Totals	897	100.1	1024	100.1
Av. length	8.93		10.05	
Sum of squares	1389		2578	

APPENDIX 12. LENGTHS OF HERRING LARVAE TAKEN IN 1951

In 1951 samples of larvae were taken at 6 sampling stations in Toquart Bay and vicinity (Fig. 9, 10). Divided into 11 periods, the length frequencies observed at each station are shown in Table R. Samples were taken at night only and above a depth of 1 fathom (1.8 m).

TABLE R. Number and percentage length frequencies of larvae taken in Toquart Bay and vicinity at six sampling stations, during 1951.

Dates	Station	Av. no. of larvae	Number measured	Length in millimetres																				
				5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Av.
Mar. 24–26	1	735	313	...	4	23	37	30	5	...	+	1	+	...	...	...	...	...	...	...	...	...	...	8.1
	2	55	75	4	13	45	32	4	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	7.2
Mar. 28–29	1	2445	400	...	+	14	42	35	7	+	+	...	+	+	...	...	...	...	...	...	...	...	...	8.2
	2	3250	200	...	+	14	42	34	7	1	...	...	1	...	...	...	...	...	...	...	...	...	...	8.4
	3	39	48	...	2	27	21	17	4	6	10	13	...	...	...	...	...	...	...	...	...	...	...	9.2
Mar. 30–31	1	302	300	...	6	37	38	14	2	...	...	1	...	...	...	...	...	...	...	...	...	...	...	7.6
	2	213	200	+	1	8	20	40	20	4	1	2	1	3	...	...	...	...	...	...	...	...	...	9.2
	3	390	300	...	1	5	22	18	17	5	3	8	12	8	1	...	...	...	...	...	...	...	...	10.5
	5	200	105	...	1	12	24	19	23	4	3	7	6	3	...	...	...	...	...	...	...	...	...	9.8
Apr. 4–5	1	310	200	...	+	+	14	41	37	6	...	...	...	...	+	...	...	...	...	...	...	...	...	9.2
	2	288	200	...	+	6	16	34	28	10	+	1	2	+	...	+	+	...	...	...	...	...	...	9.1
	3	640	100	...	...	...	5	13	26	25	19	8	...	...	1	3	...	...	...	...	...	...	...	10.9
	4	250	100	...	+	7	22	20	14	18	2	2	4	3	6	1	1	...	...	...	...	...	...	10.2
	5	360	100	...	...	1	19	30	21	9	3	2	5	9	1	...	...	...	...	...	...	...	...	10.2
	6	230	100	...	1	13	21	18	18	12	5	5	1	5	...	1	...	...	...	...	...	...	...	9.7
Apr. 8–10	1	725	200	...	...	1	10	5	20	36	16	8	+	+	1	+	...	+	1	...	...	...	...	10.6
	2	1600	301	...	...	2	7	7	22	33	21	5	1	+	+	1	+	1	...	...	...	...	...	10.8
	3	1230	300	...	...	+	2	5	21	33	25	9	1	...	...	2	1	...	...	...	...	...	...	11.2
	4	2270	100	...	...	2	1	17	28	15	18	9	2	...	1	2	3	2	...	...	...	...	...	11.2
	5	830	200	...	...	...	...	6	26	36	19	6	2	+	+	2	+	+	...	...	...	...	...	10.8
	6	440	100	...	...	1	1	5	20	36	23	7	...	1	...	3	2	1	...	...	...	...	...	11.4
Apr. 13–17	1	103	391	...	...	2	3	6	13	13	10	14	14	13	9	3	+	...	...	...	...	...	...	12.5
	2	122	313	...	...	1	6	20	13	5	6	13	16	14	14	1	...	...	...	...	...	...	...	11.8
	3	408	345	...	+	7	12	4	7	13	24	21	9	2	+	1	...	...	...	...	...	...	...	11.3
	4	529	400	...	2	20	14	3	3	9	18	18	10	2	1	+	...	...	...	...	...	...	...	10.6
	5	237	289	...	...	1	+	2	7	20	34	22	10	2	1	...	...	+	...	...	...	...	...	12.0
	6	66	113	...	1	2	2	2	8	10	24	30	15	5	1	1	...	...	...	...	...	...	...	12.4
Apr. 18–22	1	2	15	...	...	...	13	13	7	7	13	7	27	...	7	7	...	...	...	...	...	...	...	12.2
	2	2	10	...	...	...	...	10	40	10	10	30	...	...	...	...	...	...	...	...	...	...	...	11.1
	3	9	51	...	...	...	...	4	18	12	8	10	18	22	8	2	...	...	...	...	...	...	...	13.2
	4	2	8	...	...	...	...	...	25	12	12	22	25	...	...	...	...	...	...	...	...	...	...	12.0
	5	7	43	...	...	...	7	12	12	14	12	12	16	16	...	...	...	...	...	...	...	...	...	12.0
	6	1	0	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	
Apr. 23–25	1	35	241	...	...	+	+	2	12	19	12	11	10	17	11	3	1	1	...	...	...	...	...	12.9
	2	20	69	...	...	...	...	...	7	20	23	16	10	7	10	4	1	...	...	...	...	...	...	12.6
	3	41	119	...	...	...	3	...	4	7	7	4	13	19	18	18	3	3	2	...	...	...	...	14.9
	4	10	59	...	...	...	...	...	5	3	9	1	12	24	29	9	3	3	...	...	1	...	...	14.8
Apr. 29–30	1	9	49	...	...	...	...	...	2	2	14	18	27	12	12	2	6	2	2	...	...	...	...	14.1
	2	7	23	...	...	...	9	...	...	...	17	17	21	4	17	9	...	...	4	...	...	...	...	13.6
	3	19	55	...	...	4	9	9	...	...	5	16	18	9	11	5	11	2	...	...	...	...	...	13.3
	4	37	55	...	4	25	5	7	...	...	...	2	5	11	5	4	11	5	9	..	2	4	..	13.2
	5	18	84	...	1	6	2	...	...	...	2	8	10	10	10	18	18	12	4	...	...	...	...	15.1
	6	4	7	...	...	...	...	...	...	...	...	...	14	...	...	43	29	14	...	...	...	...	...	17.2
May 3–7	1	5	17	...	...	...	18	18	18	...	...	...	...	12	12	12	...	...	12	...	...	...	...	13.0
	2	7	20	...	...	10	...	35	20	...	...	10	...	10	5	5	5	...	...	...	...	...	...	11.2
	3	26	57	...	...	19	23	18	11	3	...	3	5	5	3	3	2	2	2	...	...	...	...	10.2
	4	37	140	...	2	14	21	4	26	16	2	1	2	1	3	1	1	1	4	1	...	...	...	10.3
	5	8	30	...	...	3	...	7	20	13	...	...	...	3	...	13	3	10	17	10	...	...	...	14.9
	6	6	15	...	...	13	20	7	20	7	...	...	...	...	7	7	...	7	...	13	...	...	...	12.3
May 8–11	1	4	24	...	...	...	...	8	12	33	21	4	...	...	4	8	...	4	...	4	...	...	...	12.2
	2	9	23	...	...	...	...	4	17	35	17	4	...	...	4	9	...	4	...	4	...	...	...	12.2
	3	2	8	...	...	...	...	12	12	38	12	...	...	12	...	12	...	...	...	...	...	...	...	11.7
	4	42	55	...	...	...	...	...	20	31	29	4	2	4	...	4	4	2	...	2	...	...	...	12.5
	5	42	108	...	...	...	...	1	2	4	4	4	...	...	4	10	9	15	10	20	10	6	3	19.1
	6	8	3	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	

APPENDIX 13. COMPARISON OF DIFFERENT GROUPS OF LARVAE

In 6 samples taken March 24–26, 1951, in Toquart Bay, the larvae fell into two distinct groups of 3 samples each (Table S). Three samples were taken from each group. The difference of mean lengths of the 2 groups was 1.40 mm, a highly significant difference (t = 14.0, P<0.001).

TABLE S. Length frequencies of two distinct groups of larvae in Toquart Bay on March 24–26, 1951

Length (*mm*)	Group 1			
	Sample 1 March 25	Sample 2 March 26	Sample 3 March 26	Total
5	...	...	3	3
6	4	7	10	21
7	36	26	34	96
8	19	17	24	60
9	...	2	3	5
10	...	...	...	...
11	...	...	1	1
12	...	...	...	...
13	...	...	...	...
14	...	...	...	...
Totals	59	52	75	186
Av. length	7.3	7.3	7.2	7.25
Sum of squares	...	...	...	117

	Group 2			
	Sample 1 March 24	Sample 2 March 24	Sample 3 March 25	Total
5	...	...	...	...
6	...	...	...	...
7	4	4	2	10
8	11	35	34	80
9	10	27	35	72
10	4	3	9	16
11	...	...	...	...
12	...	1	...	1
13	2	...	1	3
14	1	...	...	1
Totals	32	70	81	183
Av. length	8.9	8.5	8.7	8.65
Sum of squares	...	...	...	196

APPENDIX 14. LENGTHS OF LARVAE FROM NORTHERN BARKLEY SOUND IN 1950

Table T gives the length distributions of larvae in sectors A through G of the Sound (Fig. 11, 12). A general increase in size with time is evident, but it is complicated by the recruitment of larvae from spawnings at different times and/or places.

TABLE T. Percentage length frequencies of herring larvae from the northern part of Barkley Sound during the spring of 1950.

Sector	Number measured	Length in millimetres																					
		5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Av.
April 4–8																							
A	2724	...	+	4	18	30	26	12	7	3	1	+	...	...	...	...	...	...	...	...	...	...	9.6
B	1100	...	+	3	20	35	17	14	8	3	1	+	...	...	...	...	...	...	...	...	...	...	9.7
C	812	...	2	4	27	27	18	15	4	2	+	+	...	...	...	...	...	...	...	...	...	...	9.2
E	72	...	9	17	33	29	11	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	8.1
April 13–15																							
A	1443	...	+	1	4	5	8	21	23	18	12	5	2	+	+	+	+	...	...	...	...	...	11.8
B	300	...	...	...	+	3	6	7	8	20	20	21	9	4	...	...	...	...	...	...	...	...	13.4
C	332	...	...	2	3	4	9	11	21	18	14	11	4	3	...	...	...	...	...	...	...	...	12.5
E	789	2	5	8	8	10	8	11	14	14	11	7	2	+	+	+	...	...	+	...	...	...	10.9
F	327	2	2	7	9	6	9	13	13	13	12	8	3	...	1	...	...	1	...	...	...	...	11.5
April 18–20																							
A	798	...	...	+	1	6	7	14	15	19	14	11	6	4	1	1	...	...	...	...	...	...	12.8
B	301	...	...	+	4	11	16	7	5	12	14	12	9	5	3	1	+	...	...	...	+	...	12.6
C	25	...	...	...	4	4	4	4	12	4	24	36	...	8	...	...	...	...	...	...	...	...	13.6
D1, 2	300	...	...	2	9	11	8	5	7	12	15	15	9	5	2	...	...	...	...	...	...	...	12.6
D3-6	300	...	1	21	37	16	3	1	2	3	6	4	4	2	1	1	+	...	...	...	...	...	9.8
F	656	...	1	7	27	12	5	8	9	11	9	7	4	1	+	+	...	...	...	...	...	...	10.8
G	576	...	1	3	9	9	6	6	10	15	13	10	6	6	2	2	1	+	...	...	...	...	12.4
April 21-25																							
A	76	...	...	...	3	5	7	13	12	15	20	12	10	3	...	...	...	...	...	...	...	...	12.9
B	332	...	...	...	...	2	4	8	6	10	22	19	17	7	3	2	...	...	...	...	...	...	14.2
C	468	...	...	...	1	3	7	7	10	13	20	19	10	6	3	1	...	...	...	...	...	...	13.7
D	476	+	3	7	7	5	4	4	6	12	14	12	11	9	3	2	+	...	...	...	...	...	12.8
E	214	...	...	+	2	7	8	7	5	12	13	15	16	8	3	2	1	+	...	...	...	...	13.6
F	319	...	...	2	14	31	17	6	5	6	7	5	4	2	+	1	+	...	...	...	...	...	10.7
G	69	...	1	7	12	7	9	12	12	6	7	10	9	3	3	3	...	...	...	...	...	...	12.1
April 26-30																							
B	228	...	...	3	13	1	2	7	8	11	13	10	7	4	8	8	4	...	...	...	...	...	13.6
C	68	...	...	1	...	...	16	22	21	7	7	7	6	4	3	4	...	...	...	...	...	...	12.5
D	337	1	2	6	8	19	19	13	5	3	2	4	5	5	3	3	2	+	...	...	...	...	11.3
E	74	...	1	...	4	14	24	18	11	9	1	11	4	3	...	...	...	...	...	...	...	...	11.5
F	40	...	...	...	...	2	10	23	12	20	5	2	10	13	...	2	...	...	...	...	...	...	12.9
G	208	...	2	...	4	15	16	20	14	7	2	6	4	3	2	2	1	...	+	...	...	...	11.5
May 7-11																							
A	375	...	...	...	3	5	9	7	3	2	5	8	11	11	14	10	5	3	2	...	1	+	15.2
B	194	1	...	+	1	3	2	3	6	7	10	18	15	8	3	11	6	3	2	1	...	1	15.8
C	309	...	...	+	1	1	2	1	1	6	8	18	13	14	6	11	8	5	3	2	1	...	16.8
D	285	...	...	...	...	+	...	1	1	1	4	12	12	14	12	13	9	7	5	4	4	2	18.4
E	240	...	...	...	+	...	1	+	1	3	6	15	15	20	10	10	7	6	4	2	...	1	17.4
F	247	...	...	...	...	...	+	...	1	2	5	16	16	13	12	9	8	9	4	4	1	...	17.6
G	36	...	...	...	...	...	...	...	...	3	...	11	20	22	6	8	8	8	...	11	3	...	18.1

APPENDIX 15. DIFFERENCES IN LARVAL ABUNDANCE

The numbers of larvae in samples taken in mid-April are shown in Table U, for two regions: the Forbes Island and Chrow Island sectors, and the Outer Hankin Island sector. The asymmetry of the frequency distribution of the former makes it impossible to test for differences by a simple *t*-test, but the Hankin Island samples obviously have fewer larvae, on the whole. A *t*-test on the logarithms of the values tabulated will confirm the significance of this difference.

TABLE U. Number of larvae in samples in (1) the Forbes Island and Chrow Island sectors April 13-15 and April 18-20, 1950, and (2) in the outer Hankin Island sector for the same periods.

Dates	Number of larvae taken per sample	
	Forbes I. and Chrow I.	Outer Hankin I.
April 13–15	2350 (Forbes I.)	60
	470 "	102
	310 "	70
	680 "	60
	290 "	...
	190 "	...
April 18 20	2000 (Chrow I.)	110
	750 "	200
	340 "	75
	530 "	55
	475 "	...
	160 "	...
Average	712	92

APPENDIX 16. NET TRANSPORT OF WATER IN BARKLEY SOUND IN APRIL, 1950

TABLE V. The net transport of water at the surface and at depths of 3, 5, and 10 fathoms at various stations in Barkley Sound in April, 1950. (From data of Doe, 1952).

Oceanographic station	Corresponding larval sampling station			Date (April)	Net transport of water in nautical miles per tidal day (25 hr)				
	Sector		Station		Surface	3 *fa* 5.5*m*	5 *fa* 9.2*m*	10 *fa* 18.3*m*	Av.[a]
6	Toquart Bay	(A)	6	21–22	1.0	0.9	0.3	0.9	0.8
39	Mayne Bay	(C)	2	25–26	2.0	1.6	1.4	0.1	1.3
5	Mayne Bay	(C)	6	17–18	1.4	0.4	0.9	0.0	...
15	Nettle I.	(D)	4	12–13	1.4	3.0	2.3	1.5	2.0
24	Hankin I.	(F)	5	19	3.9	1.0	1.1	2.6	...
				24	2.2	0.4	1.2	0.8	...
23	Forbes I.	(E)	5	22–23	4.3	2.4	2.3	0.8	2.4
25	Chrow I.	(G)	1	20–21	7.7	4.5	2.9	2.0	4.9

[a] Average net transport given only for stations at which movement of water at all depths was in the same general direction.

APPENDIX 17. RATE OF DECREASE OF LARVAE IN TOQUART BAY

It is possible to follow the decrease of herring larvae in Toquart Bay over two periods in 1950. The original brood was sampled over the period April 6–10 to April 26–30, or 25 days (Fig. 16). In Table W, upper half, these are divided into five 5-day periods. The average number of larvae per sample decreases rapidly. The least-squares slope of the logarithm of the number against time in days is −0.18, so that the rate of survival is antilog 1.82 = 0.66 per day. The average rate of decrease is 34% per day (instantaneous rate = 0.41).

Later broods can be followed from May 6–10 to May 21–26 (Table W, lower half). The slope of the logarithms is −0.11 per day, rate of survival = 0.78 per day, and rate of decrease is 22% per day (instantaneous rate = 0.25).

Table W. Decrease of larval broods in Toquart Bay. Period 0 is April 6–10, 1950; period 5 is April 11–15, etc.

Time in 5-day periods	No. of samples	Av. no. of larvae per sample	Logarithm
	(1) *Original larval brood*		
0	17	6150.0	3.79
5	11	1416.4	3.15
10	18	91.2	1.96
15	14	10.3	1.01
20	2	3.0	0.48
	(2) *Later larval broods*		
30	17	35.1	1.55
35	12	7.3	0.86
40	21	2.5	0.40
45	6	0.7	−0.15

APPENDIX 18. DISAPPEARANCE OF THE LARVAL YOLK SAC

Table X gives details of larvae caught and percentage with yolk sac, in individual samples taken from Queen Cove in 1949. Table Y relates the average figures to the length of the larvae.

Table X. Percentage of larvae bearing yolk sacs (A), and number of larvae per sample (B), on 5 different days at Queen Cove, in 1949.

March 31		April 3		April 7		April 13		April 18	
A	B	A	B	A	B	A	B	A	B
99	91,000	69	15,700	34	3,600	5	500	0	14
93	23,400	66	5,500	20	3,950	0	1,280	0	250
90	7,100	51	3,200	19	2,330	3	415	0	410
85	8,850	65	3,550	19	5,850	0	500	0	270
83	3,750	63	15,600	16	4,700	2	740	0	215
93	3,100	60	5,400	24	13,500	2	1,090	...	...
94	10,800	...	...	17	1,410	0	1,200	...	...
...	...	...	...	16	1,100	1	400	...	...
...	...	...	...	14	1,360	0	164	...	...
...	...	...	...	...	...	1	310	...	...

TABLE Y. Average number of larvae per sample, percentage of them with yolk sac, and their mean and modal lengths, for the samples of Table X.

	31.iii	3.iv	7.iv	13.iv	18.iv
Larvae per sample	21,100	8,160	4,090	670	232
With yolk sac (%)	91	62	20	1.4	0
Mean length (*mm*)	8.7	9.1	10.2	12.1	13.0
Modal length (*mm*)	8	9	10	12	13

APPENDIX 19. MARCH SNOWFALL, AIR TEMPERATURE AND SIZE OF YEAR-CLASSES

TABLE Z. March snowfall at Goldstream Lake, relative strength of herring year-classes (from Appendix 2), and average air temperature at Pachena Point for March and April. Snowfall and temperature data are from "Climate of British Columbia", British Columbia Department of Agriculture, Victoria, B.C. (issued annually); the quantity of snow tabulated is equivalent rain.

Year	Snowfall		Year-class strength	Air temperature			
				March		April	
	inches	*mm*		°F	°C	°F	°C
1936	18.5	470	64	40.7	4.8	45.7	7.6
1937	2.7	69	142	44.7	7.1	44.7	7.1
1938	28.7	728	82	41.3	5.2	47.0	8.3
1939	22.8	579	46	43.2	6.2	47.0	8.3
1940	2.0	51	26	46.3	7.9	49.8	9.9
1941	0.0	0	61	48.3	9.1	49.7	9.8
1942	10.0	254	115	42.7	5.9	47.3	8.5
1943	4.4	112	429	41.7	5.4	47.7	8.7
1944	1.5	38	263	43.0	6.1	47.3	8.5
1945	8.0	203	235	43.0	6.1	45.7	7.6
1946	6.3	160	198	42.3	5.7	45.3	7.4
1947	0.3	8	307	46.3	7.9	47.7	8.7
1948	8.3	211	102	42.0	5.6	44.7	7.1
1949	5.5	140	128	44.0	6.7	45.7	7.6
1950	21.6	548	135	41.7	5.4	44.0	6.7

Record of the Oceanic Puffer, *Lagocephalus lagocephalus* (L.), Family Tetraodontidae, from Newfoundland[1]

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ABSTRACT

A female specimen of *Lagocephalus lagocephalus* (L.), 60 cm long, was collected alive on Aug. 26, 1961 on the beach at Point Verde, Placentia Bay, Newfoundland, 47°14′N, 54°01′W. This is apparently the first record of this species in the western Atlantic.

INTRODUCTION

On aug. 26, 1961 a female specimen of the oceanic puffer, *Lagocephalus lagocephalus* (L.), 60 cm long, drifted onshore on the beach at Point Verde, Placentia, Placentia Bay on the southeast coast of Newfoundland, Lat. 47°14′N, Long. 540°1′W. The fish was washed in by a heavy sea and was alive when captured by Mr Charles Walsh of Point Verde. It was frozen very soon afterwards and brought to the Biological Station in the frozen condition on Aug. 28 by Mr Leo Walsh. It was then thawed and examined in an excellently fresh condition by the author (Fig. 1).

The Point Verde *Lagocephalus. lagocephalus* of Fig. 1 is different in ventral anterior outline from the drawings of this fish in the uninflated condition given in Ramalho (1931a) and in Smith (1949), and from the artist's conception of the inflated condition in the former publication in that it is more inflated anteriorly. Observation of the degree of exposure of the ventral spines from the spine grooves in Fig. 1 indicates that anteriorly the ventral air pocket is expanded and that posteriorly there is little or no expansion of the air pocket to obliterate the grooves and project the spines.

The Point Verde fish was drifted ashore probably with the air pocket somewhat filled with air and was frozen in this condition so that when thawed the anterior region did not contract to a life-like uninflated condition.

Blowing up the anterior air pocket of the thawed fish to its maximum retention point by passing compressed air into the oesophagus produced the shape shown in Fig. 2 with the anterior ventral portion considerably inflated and the abdominal region still with deep spine grooves and relatively uninflated.

DESCRIPTION

Because the Point Verde *Lagocephalus lagocephalus* is apparently the first of this species to be captured on the western side of the Atlantic and the only

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individual of the genus *Lagocephalus* to be reported from eastern Canadian waters, and because available descriptions of *L. lagocephalus* are lacking in essential information the specimen has been reported in some detail. Its general characteristics are shown in Fig. 1–7.

The colour of the Newfoundland specimen is purplish-black above, fading into purplish at upper flanks; brownish, darkish and whitish patches on flanks, white on belly; fins, including caudal, mainly dark, with pectoral lightish ventrally, grey below pectoral; a white spot (about 1 cm diameter, with several black spots included) on top of the head just behind the nostrils. The skin spines are strong and moderately blunt. Skin on back and flanks smooth with no spines. Spines extend ventrally in transverse and longitudinal rows from below throat to in front of cloaca (Fig. 4). Each spine has a cross-shaped base (Fig. 3) embedded in the subcutaneous tissue parallel to surface of skin. Spines mostly 2–3 mm high. No true teeth but bones of upper and lower jaws form 2 large sharp plates, each divided by a suture (Fig. 5). One gill cleft on each side through skin to exterior in front of base of pectoral. Three sets of gills on each side plus anterior small pseudobranch, and a fourth gill arch, without a gill, attached to the posterior wall of the branchial cavity. Stomach empty. Female maturing, eggs opaque, egg diameter 0.5 mm, weight of ovary 765 g (Fig. 6). Possesses anterior ventral air pocket with a black lining. In the relaxed condition this pocket begins below the head and extends backward dorsally to the bases of the pectoral fins and ventrally to slightly beyond the posterior ends of the pectoral fins (Fig. 6). This pocket can be distended by air or water to produce a puffed-up appearance (Fig. 2). There are no ventral fins.

The lateral line—noticeable as a fine black line (Fig. 7)—extends from the base of the caudal in a wavy line, more or less medially, to between the dorsal and anal fins, then rises dorsally to pass well above the upper base of the pectoral fin. In front of the pectoral it descends again and forms a loop encircling the orbit and passing behind and anteriorly below the nostril. About one-third of the distance between the base of the pectoral and the eye a branch passes dorsally and transversely on the neck to join the lateral line on the other side. About midway between the posterior border of the orbit and the gill slit another branch passes somewhat vertically ventrally along the cheek to the beginning of the spiny region.

The second lateral line on the lower part of the tail mentioned by Smith (1949) as characteristic of the genus *Lagocephalus* but not of the related *Sphaeroides* may be present as the white line with several large and other smaller pores extending ventrally from the root of the caudal forward almost to the anal fin (Fig. 7). The raised ventro-lateral skin fold also noted by Smith as characteristic of *Lagocephalus* and indicated in the figure given in Ramalho (1931a) was noticeable (Fig. 7) but was not very well developed in this specimen.

In the following detailed description, unless otherwise noted, all measurements of the Newfoundland specimen are horizontal lines between vertical planes and are of the specimen in the relatively uninflated condition of Fig. 1. Unless otherwise stated all information in square brackets refers to comparative data

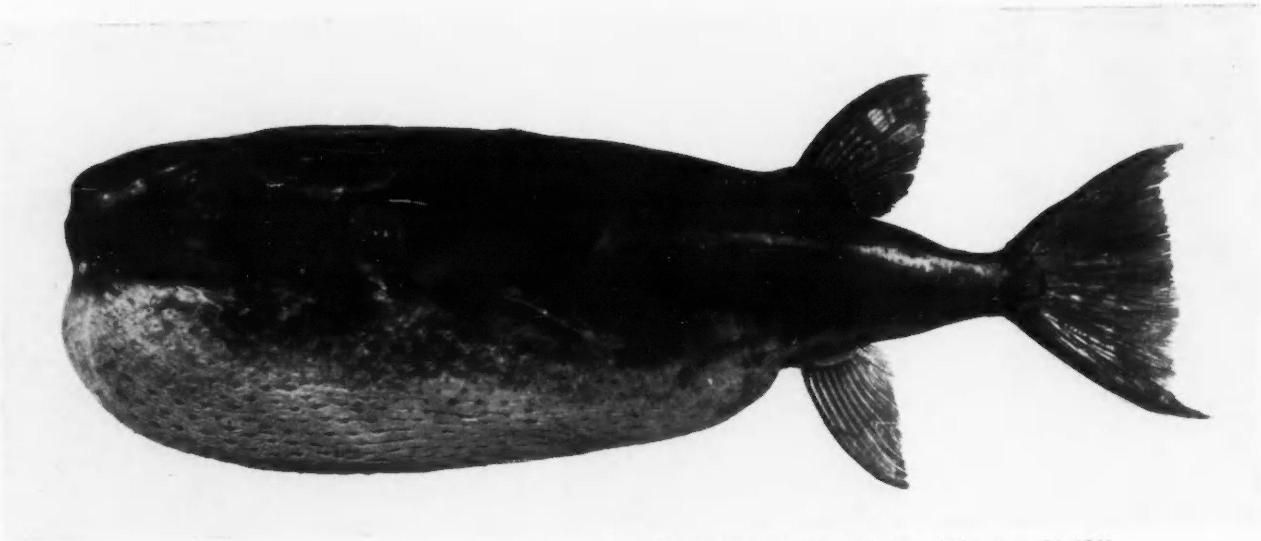

FIG. 1. *Lagocephalus lagocephalus* collected at Point Verde beach, Placentia Bay, Nfld., Aug. 26, 1961.

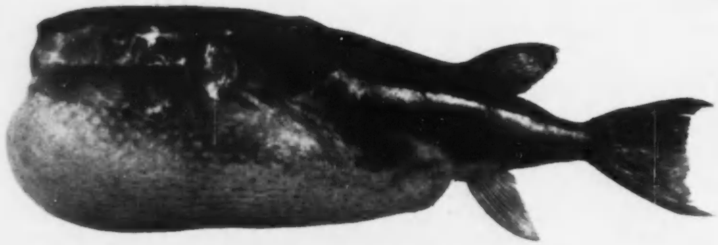

Fig. 2. Point Verde specimen of *Lagocephalus* with anterior air pocket inflated by inserting air hose in oesophagus.

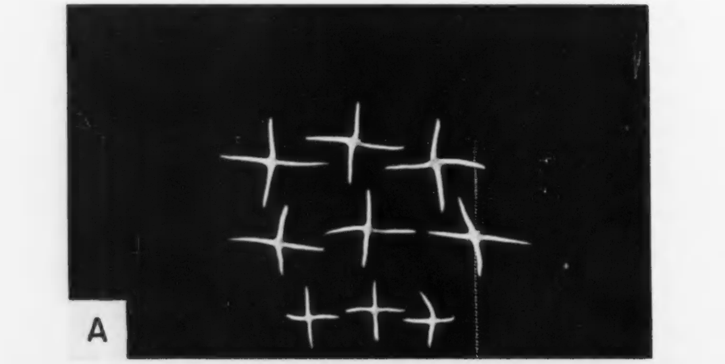

Fig. 3. Body spines of the Point Verde specimen of *Lagocephalus* showing the cross-shaped roots: (A) approximately natural size, camera vertical, (B) ×2 and photograph taken obliquely to show better the spines which protrude through the skin.

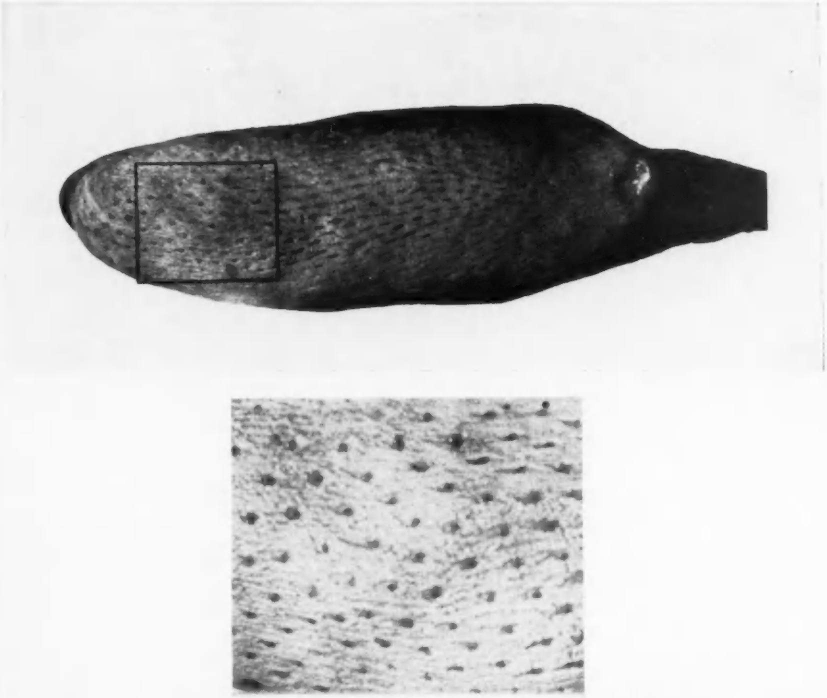

FIG. 4. Ventral view of the Point Verde specimen of *Lagocephalus* showing distribution of spines from chin to cloaca.

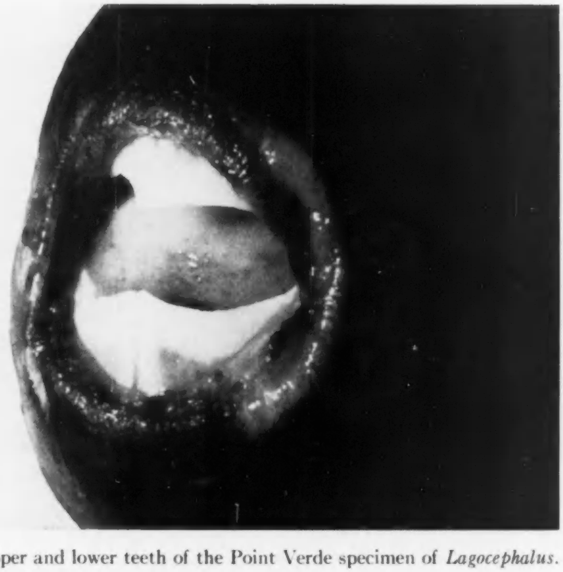

FIG. 5. Upper and lower teeth of the Point Verde specimen of *Lagocephalus*.

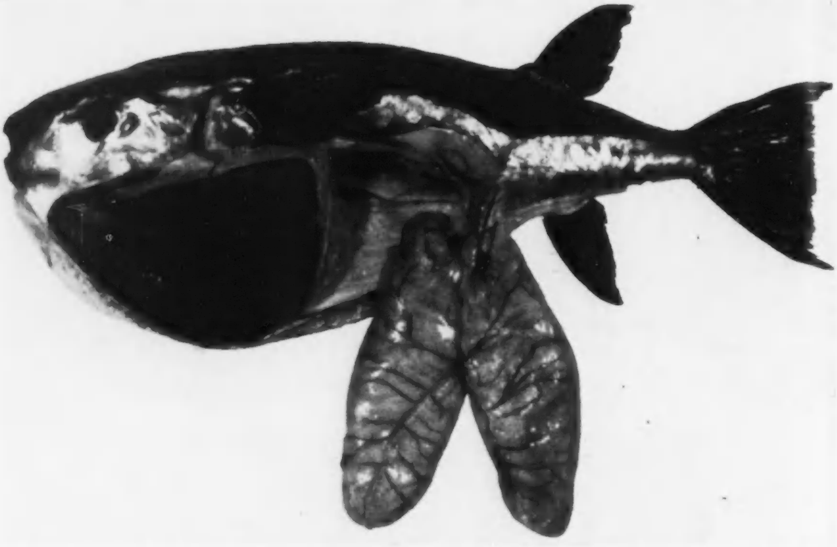

FIG. 6. Dissected Point Verde specimen of *Lagocephalus* showing ovaries and the dark-lined inflatable antero-ventral pocket. (In this photograph the pocket is somewhat artificial in shape, being held open by a strip of plastic.)

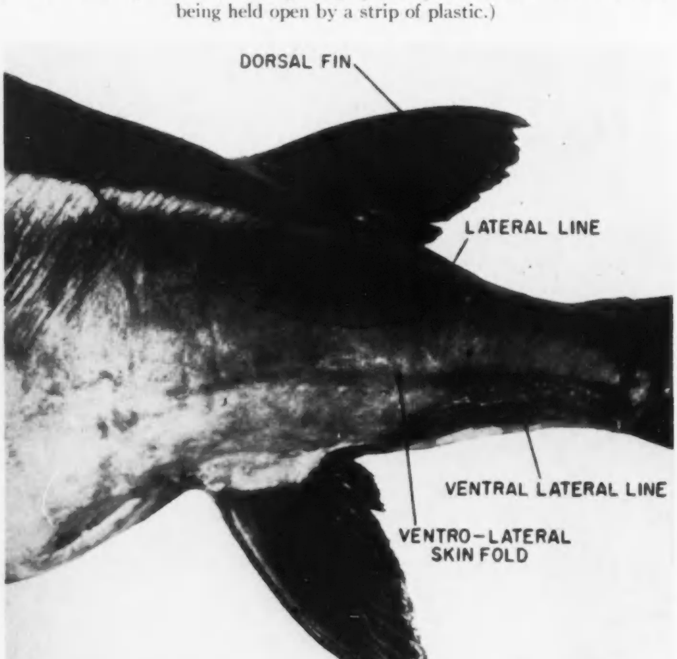

FIG. 7. Caudal region of Point Verde specimen of *Lagocephalus* to show lateral line (fine black line), lower lateral line? and skin fold in tail region. (This photograph was taken with the fish inclined to show the lower lateral line to best advantage. Thus the upper lateral line and the ventro-lateral skin fold appear to be situated more dorsally than they actually are. See Fig. 1 and 2 for indication of actual position of upper lateral line between dorsal and anal fins.)

on European specimens from Ramalho (1931a). The methods of taking body-proportion measurements for these European specimens are not known to us.

Whole weight, 3.5 kg. Total length: snout to mid-fork, 60.2 cm [up to *ca.* 50 cm. (At least 60 cm, Smith, 1949)]; snout—tips dorsal and ventral lobes caudal fin, with caudal lobes extending directly backward to their greatest length, 62.8 (+ estimated 0.8 cm missing) and 64.5 cm respectively [ventral lobe of caudal longer than dorsal lobe]; standard length, snout—root of caudal in mid-line, 53.0 cm. Head length: snout—posterior (ventral with skin slit) end operculum, 15.8 cm, direct line, 16.2 cm. Greatest length orbit, 3.3 cm; longitudinal diameter eyeball, 2.8 cm; longitudinal diameter eye, cornea only, 2.0 cm. Snout—anterior border orbit, 6.7 cm, direct line, 6.8 cm; snout—mid-cloaca, 37.3 cm; snout—base 1st ray dorsal fin, 38.5 cm; snout—base 1st ray anal fin, 39.9 cm. Body depth at base of pectorals, 17.4 cm. Dorsal fin: 1st ray longest, length 1st ray, 9.6 cm; 1st dorsal length at base near body, 5.4 cm, at actual base of fin rays, 4.5 cm. Length longest ray caudal (ventral), 12.5 cm. Height of gill slit, 4.5 cm.

Longitudinal diameter eyeball in head length (direct line), 5.8 [eye, 5.5–6.5]. Snout direct line—anterior border orbit in interorbital space (least fleshy width), 1.01 [*ca.* 1]. Head length (direct line) in standard length, 3.3 [3.3–3.5]. Head length in snout—base 1st ray dorsal fin, 2.44 [2.5]. Head length in snout—base 1st ray anal fin, 2.52 [2.6].

Rays: dorsal, 15 + (anteriorly) basal portion of 1 ray embedded in skin and provided with articulating muscles but no external ray [14–15]; anal, 14 [12–13]; pectoral, left, 15, right, 16 [15–16]. Vertebrae, 17 (not including urostylar half-vertebra in Newfoundland specimen, at least) [17, Smith, 1949]. Skin spines: number longitudinal rows at level of bases of pectorals, 29 [20–25]; number of transverse rows chin–cloaca, 31 [32, from figure, Ramalho, 1931a]; spine roots, 4 in cross shape [4, cross shaped]. Nostril openings, 2 pairs [2 pairs].

DISCUSSION AND CONCLUSIONS

Lagocephalus lagocephalus is rare on the Atlantic coasts of northern Europe but more common to the south. It is found in the Mediterranean, Morocco and the African tropical Atlantic (Ramalho, 1931a). Smith (1949) says that in the South African region this species, which is widespread in the Atlantic and Indian Oceans, has been found from the Cape to Natal and is sometimes seen in estuaries, but is primarily pelagic.

The only other species which could occur in the Newfoundland area, and with which *Lagocephalus lagocephalus* might be superficially confused, is *Lagocephalus laevigatus* (L.). The latter occurs on the American side of the Atlantic from Cape Cod to Brazil; it is common southward but rather rare north of Cape Hatteras (Jordan and Evermann, 1898), and also occurs on the European side off the coasts of Mauritania and Morocco (Ramalho, 1931b).

The Newfoundland specimen is, however, well differentiated from *L. laevigatus* by the usual differences between *L. lagocephalus* and this species: smaller eye, larger number of dorsal and anal and smaller number of pectoral fin rays, heavier body spines, relatively greater interorbital space, dorsal and anal fins situated more posteriorly, ventral lobe of caudal longer than superior (shorter than superior in *L. laevigatus*) and especially by the 4 roots to the body spines shown in Fig. 3 (only 3 roots in *L. laevigatus*). It also agrees generally in body proportions and other characteristics with those reported for European specimens of *L. lagocephalus*. The Newfoundland specimen, however, has more longitudinal rows of spines (29) than are reported for European specimens of *L. lagocephalus* (20–25) but we do not know how many European specimens have been examined for this characteristic.

Very likely this Newfoundland specimen of *Lagocephalus lagocephalus* originated along the North African coast, passed southward in the Canary Current and proceeded, with the general circulation of the area, westward in the North Equatorial Current toward the West Indies, northward in the Gulf Stream to south of Newfoundland where it became dissociated from the Gulf Stream and entered the surface waters of the Newfoundland area.

ACKNOWLEDGMENT

The photographs are by Mr E. L. Rowe.

Note added in proof

After this paper was submitted for publication, the following information was received from Mr G. Palmer, of the Fish Section of the British Museum of Natural History: "Fraser-Brunner (1943) gives a diagrammatic representation of the lateral lines of Lagocephalidae. An examination of 5 specimens of *L. lagocephalus* from the eastern Atlantic shows that the presence of a lower lateral line is not always easy to distinguish, as is also the case with the raised ridge which is usually present. It would appear, however, that the position of the lower lateral line is more or less as indicated on your photograph. So far as I can judge from the specimens examined the number of longitudinal rows of spines is quite variable. I do not think, therefore, that too much significance need be attached to this particular character in the present instance".

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Migration and Feeding of the Gray Whale (*Eschrichtius gibbosus*)[1]

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ABSTRACT

Observations of gray whales from the coasts of British Columbia, Washington, and Alaska are compared with published accounts in order to re-assess knowledge of migration and feeding of the American herd. Source of material is mainly from lighthouses and lightships.

The American herd of gray whales retains close contact with the shore during migration south of Alaska. Off Washington and British Columbia the northward migration begins in February, ends in May, and is at a peak during the first two weeks in April; the southward migration occurs in December and January, and is at a peak in late December. Northward migrants stop occasionally to rest or feed; southward migrants are travelling faster and appear not to stop to rest or feed during December and January. Gray whales seen off British Columbia, sometimes in inside protected waters, from June through October, probably remain in this area throughout the summer and fall months.

Available evidence suggests that gray whales retain contact with the coast while circumscribing the Gulf of Alaska, enter the Bering Sea through eastern passages of the Aleutian chain, and approach St. Lawrence Island by way of the shallow eastern part of the Bering Sea. Arriving off the coast of St. Lawrence Island in May and June the herd splits with some parts dispersing along the Koryak coast and some parts continuing northward as the ice retreats through Bering Strait. Gray whales feed in the waters of the Chukchi Sea along the Siberian and Alaskan coasts in July, August and September. Advance of the ice through Bering Strait in October initiates the southern migration for most of the herd. In summering areas, in northern latitudes, gray whales feed in shallow waters on benthic and near-benthic organisms, mostly amphipods.

There is no evidence to indicate that gray whales utilize ocean currents or follow the same routes as other baleen whales in their migrations. Visual contact with coastal landmarks appear to aid gray whales in successfully accomplishing the 5000-mile migration between summer feeding grounds in the Bering and Chukchi Seas and winter breeding grounds in Mexico.

Reconstruction of the migration from all available data shows that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December.

INTRODUCTION

The gray whale (*Eschrichtius gibbosus*) is at present found only in the North Pacific Ocean and the adjacent Bering, Chukchi and Okhotsk Seas. It is represented by two herds. An American herd alternates between winter breeding grounds in the lagoons of Mexico and summer feeding grounds in the Bering and Chukchi Seas; an Asian herd alternates between winter breeding grounds along the south and west coasts of Korea and the Okhotsk Sea.

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Gray whales have been seriously reduced by excessive exploitation and, since 1937, their capture has been prohibited by international agreement. Consequently, the species has afforded neither opportunity nor an important practical need for careful biological study in recent years. Knowledge of the gray whale's migrations and distribution, however, are perhaps better known than that of any other stock of baleen whales, because of the species' predilection to shallow coastal waters for calving, migrating and feeding, and because of precision in the timing of its migrations.

This paper deals primarily with migrations of the American herd and secondarily with supplementary considerations of feeding and route-finding. Basic knowledge of the migrations, feeding areas and breeding areas of this herd was first described by Scammon (1874). Following a period of excessive exploitation during the last part of the 1800's the species was thought to be extinct on the American Coast. Its reappearance in recent years has led to renewed interest and several papers describing behaviour, migration, and population growth, have been published since 1954. Accumulated knowledge has not been sufficient to describe the entire migration route with certainty, however, and too few stomachs have been examined to confidently describe feeding habits of the species.

This paper describes observations of gray whales mostly during the northward migration along the coasts of Washington and British Columbia, and during their feeding period in the Bering and Chukchi Seas. These observations provide information which is used, in conjunction with published accounts, to re-assess the extent of knowledge on migration and feeding habits.

SOURCES OF INFORMATION AND ACKNOWLEDGMENTS

Observations are based chiefly upon the returns of log-book sight records from lightships and lighthouses along the coasts of Washington and British Columbia. Among these are included: Umatilla, Columbia River and Swiftsure Lightships; and Kains Island, Cape St. James, Langara, Amphitrite and Cape Beale Lighthouses (Fig. 1). The co-operation of personnel manning these light stations is gratefully acknowledged.

Dr Francis H. Fay, during the course of walrus studies in the vicinity of St. Lawrence Island, has kept notes on all whales observed. His permission to use these records and to examine and report on the stomach contents of two gray whales captured by the natives of this region is gratefully acknowledged. Mr T. H. Butler, Dr D. B. Quayle and Mr and Mrs Cyril J. Berkeley, of the Biological Station in Nanaimo, B.C., kindly identified the contents of these stomach samples.

Records of gray whales sighted by Department of Fisheries personnel, especially those from the C.G.S. *Laurier*, and by Mr W. F. Hausner of the tug *Neptune*, are greatefully acknowledged.

Supplementary observations by biologists and technicians aboard the M.V. *Pacific Ocean*, chartered for pelagic fur seal research from 1958 to 1961, are included.

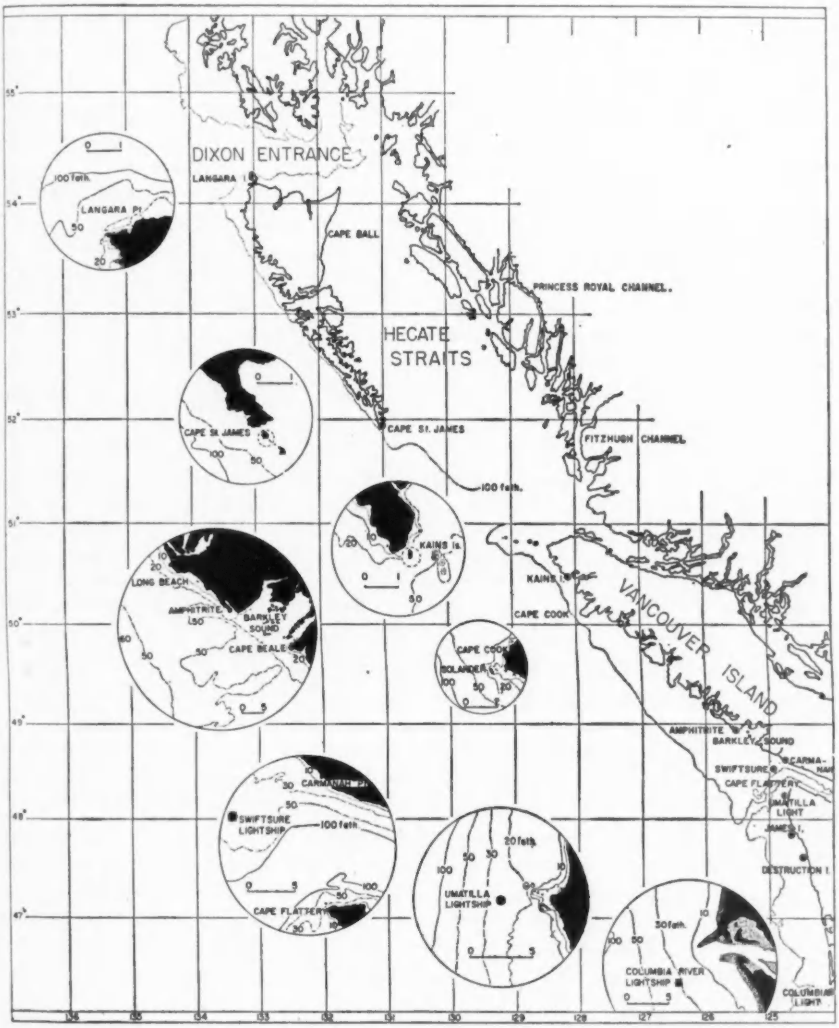
55°
54°
53°
52°
51°
50°
49°
48°
47°
DIXON ENTRANCE
LANGARA I.
100 fath.
LANGARA Pt.
50
20
CAPE BALL
PRINCESS ROYAL CHANNEL
HECATE STRAITS
CAPE St. JAMES
100
50
FITZHUGH CHANNEL
100 fath.
20
10
KAINS Is.
50
LONG BEACH
AMPHITRITE
BARKLEY SOUND
CAPE BEALE
KAINS I.
CAPE COOK
SOLANDER
VANCOUVER ISLAND
AMPHITRITE
BARKLEY SOUND
CARMANAH
SWIFTSURE
CAPE FLATTERY
UMATILLA LIGHT
JAMES I.
DESTRUCTION I.
CARMANAH Pt.
SWIFTSURE LIGHTSHIP
100 fath.
CAPE FLATTERY
20 fath.
UMATILLA LIGHTSHIP
30 fath.
COLUMBIA RIVER LIGHTSHIP
COLUMBIA LIGHT
136
135
134
133
132
131
130
129
128
127
126
125

FIG. 1. Locations of gray whale observations along the coasts of Washington and British Columbia.

OBSERVATIONS OFF WASHINGTON

An estimated 500 to 1000 gray whales pass within sight of the Umatilla Lightship on their northward migration each year from March into May. This lightship is located 4½ miles[2] from shore near Latitude 48°10′N. Many whales pass by close to shore where their presence is difficult to detect against the surf breaking along the rocky coast and boiling over Umatilla reef. Many, however, pass by close to the lightship and sometimes remain in the vicinity for periods up to 4 hours. At these times their behaviour is variously described as "playing", "mating", "circling", "rolling" or "feeding". On several occasions the whales occupied their respite in rubbing themselves gainst the anchor chain.

In 1958 gray whales were seen from the Umatilla Lightship almost every day from March 16 to April 11; none was seen in May although sighting conditions were good. In 1959 gray whales were seen from this lightship almost every day from March 15 to May 14; the last northbound whale was seen on May 29. The peak of the migration at this latitude occurs during the first 2 weeks in April and is earlier in some years than in others. Few are seen at other times of the year. Six have been reported in December and 4 in January, mostly travelling southward.

Gray whales are seldom seen from the Columbia River Lightship during the northward migration. More are seen during the southward migration in December and January. Reports for these months include: 2 in late January, 1958; 2 in late January, 1959; 8 in early January, 1960; 5 in late December, 1960; and a school on January 11, 1960. Most northward migrants probably pass shoreward of this vessel which is stationed about 6 miles off. The *Pacific Ocean* encountered many gray whales 5 to 10 miles north of this lightship on March 12, 1958; at least 10 blows could be seen at any one time; all were within 6 miles of shore and most were close to the beach. During this same month, only 2 gray whales were reported from the Columbia River Lightship.

The *Pacific Ocean* conducted fur seal research off the coast of Washington in March, April and May, 1958 to 1960, inclusive. Waters up to 20 miles from shore were hunted intensively. Only once were gray whales seen more than 10 miles from shore; 2 adults and a calf were seen 20 miles off Cape Flattery on March 19, 1959. Gray whales were frequently encountered while the vessel lay at anchor or passed close to shore in transit to and from port; few were seen farther than 6 miles from shore; most appeared to be travelling within a mile of the coast where their presence was difficult to detect against the breaking surf. Important observations of gray whales from this vessel include: many between Gray's Harbor and Destruction Island from April 6 to 22, 1959; 20 to 30, 5 miles off Cape Flattery on March 27, 1958; and 50 between Destruction Island and Cape Flattery on March 27, 1960. While the vessel lay at anchor in shallow water off Raft River, Washington, whales could be heard blowing and splashing throughout the night of April 5–6, 1960.

The *Laurier* estimated 150 gray whales travelling close to shore between Destruction Island and Cape Flattery on April 1, 1958.

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[2] Distances in this paper are given in nautical miles. 1 nautical mile = 1.855 km; 1 knot = 1 nautical mile per hour.

TABLE I. Observations of gray whales off Washington, 1958–60.

Location and vessel	Date	Remarks
	1958	
5–10 mi north of Columbia River; *Pacific Ocean*	Mar. 12	At least 10 blows seen at any one time; mostly northbound
5 mi off Cape Flattery; *Pacific Ocean*	Mar. 27	20–30 northbound gray whales
Destruction Island to Cape Flattery; *Laurier*	Apr. 1	150; mostly gray whales; close to shore; all northbound
Umatilla Lightship	Mar. 16–Apr. 11	Estimated 500–1000; all northbound; seen almost every day
Umatilla Lightship	May	Visibility good, but no whales seen
Umatilla Lightship	Dec. 10–31	6 whales, thought to be grays, southbound
	1959	
Umatilla Lightship	Jan. 18–19	4 gray whales; southbound
Umatilla Lightship	Mar. 15 29	Gray whales almost every day; all northbound; mostly from March 28 to April 12
Umatilla Lightship	Dec. 16–17	7 or more gray whales; southbound
Umatilla Lightship	Dec. 25–28	5 unidentified whales; probably grays; southbound
Columbia River Lightship	Jan. 21 .	2 gray whales; southbound
Gray's Harbor to Destruction Island; *Pacific Ocean*	Apr. 6–22	Many northbound gray whales
20 mi off Cape Flattery; *Pacific Ocean*	Mar. 19	3 gray whales: 2 adults, 1 calf
	1960	
Columbia River Lightship	Jan. 1–5	8 southbound gray whales
Columbia River Lightship	Jan. 11	School of southbound gray whales
Columbia River Lightship	June 30	1 southbound gray whale
Columbia River Lightship	Dec. 28–30	2 gray whales circling vessel
Destruction Island to Cape Flattery; *Pacific Ocean*	Mar. 27	50 gray whales en route; some feeding near Destruction Island
Near Destruction Island; *Pacific Ocean*	Apr. 5	Few northbound gray whales travelling both inside and outside Destruction Island
Mouth of Raft River (Lat. 49°20′N); *Pacific Ocean*	Apr. 5–6	Many gray whales blowing throughout night; very active in shallow water

OBSERVATIONS OFF BRITISH COLUMBIA

After leaving the Washington coast at Cape Flattery, gray whales cross the Strait of Juan de Fuca in a general northerly direction before changing course westerly to follow the west coast of Vancouver Island. Gray whales are frequently seen by coastal vessels close to shore between Carmanah Point and Barkley Sound, but few are seen from the Swiftsure Lightship located 8 miles off the coast.

Off Cape Beale, which is located at the lower entrance to Barkley Sound, gray whales sometimes stop to play or feed during the northward migration in March and April. After rounding Cape Beale some may enter the Sound for a short distance and have been seen rubbing themselves against the rocks along Folger Island. Most of the herd proceeds directly across the 15-mile mouth of the Sound towards Amphitrite Point, following closely along the outer edges of a group of rocks lying part way across; a few enter narrow channels between these rocks. Most of the northward migrating whales pass Amphitrite Point shoreward of a buoy which lies about 1 mile off the light. Some have been seen rubbing themselves against the lines which moor this buoy.

The lightkeeper at Amphitrite Point, former whaler, reports that almost 1000 gray whales pass northward within sight of the lighthouse each spring, mostly in March and April, but in some years beginning in February and in other years ending in May. He has never seen them travelling southward.

During the course of fur seal hunting in 1958, gray whales were seen at the mouth of Barkley Sound and along Long Beach almost every day from March 14 to April 30. Some were seen moving back and forth along Long Beach as though feeding and some were seen rubbing themselves against Long Beach Rocks and Florencia Island, both of which lie about 1½ miles off the sandy beach. No gray whales are seen more than 2 miles from shore in this locality although fishing activity and ship traffic are fairly heavy during the migratory period.

Whalers from the Coal Harbour whaling station, while passing in and out of Quatsino Sound, report that gray whales are seen following closely along the shoreline but are never encountered on the whaling grounds which extend from 10 to 100 miles offshore. While rounding Cape Cook, gray whales pass inside Solander Island, a rock located 1 mile off Cape Cook.

When crossing the mouth of Quatsino Sound, some gray whales enter the Sound for a short distance before regaining the shore near Kains Island Light. Northbound gray whales pass this lighthouse mostly during the second and third week in April at which time approximately 5 per day are seen, travelling close to shore at a rate of about 4 knots.

The scarcity of sightings of gray whales on the southward run along the west coast of Vancouver Island in winter is chiefly a result of poor weather which discourages coastwise shipping and makes observation difficult. Only three noteworthy reports of southward migrants along this coast have yet appeared. A whaling captain, Mr Einar Jensen, reports a school of gray whales travelling southward off Long Beach in January, 1953. Another whaling captain, Mr Harold Sampson, saw gray whales travelling southward off the west coast of Vancouver Island, December 15 to 20, 1955. Eighty gray whales, all travelling southward, were sighted from the Kains Island Lighthouse during a period of exceptionally good weather from December 15 to January 4, 1955–56. Up to 21 whales per day were seen on and near December 17. Some of these whales entered the Sound for a short distance or tarried briefly near the rocks.

The route taken by gray whales on leaving the north end of Vancouver Island is not known. The few observations available suggest that the whales may become temporarily confused in crossing this broad 120-mile stretch of water between Vancouver Island and the Queen Charlotte Islands. On April 7, 1958, 8 gray whales were sighted from the *Pacific Ocean* 10 miles east of the Cape St. James Light. Two gray whales were sighted from the *Laurier* 5 miles east of Cape Ball in northern Hecate Strait on April 23, 1958. The outer coast of Cape St. James is largely obscured from view from the lighthouse. Consequently, few gray whales are seen from this station. The few which have been sighted at the time of the northward migration in April appeared to be travelling southward along the Hecate Strait shoreline to re-enter the Pacific by way of a narrow channel which isolates the island on which the lighthouse is located.

Few gray whales are seen along the uninhabited west coast of the Queen Charlotte Islands during the northward migration. Some are seen from the Langara Island Lighthouse which is located near the northwest tip of the Islands. This lighthouse is, however, poorly located for observing gray whales, which may pass some distance offshore in commencing the crossing of Dixon Entrance. More are seen at times other than spring months, suggesting that some gray whales may linger in the vicinity of Langara Island throughout the summer and fall feeding season. Southbound gray whales are seen here from September through January, but mostly in December. During summer and fall months, the direction of travel is variable.

Two reports by reliable observers show that gray whales occasionally enter inland passages in British Columbia during summer months. The *Laurier* reports one gray whale in Princess Royal Sound on August 1, 1958, and one in Fitz Hugh Sound on August 2, 1958.

No gray whales are reported by research vessels operating offshore of Vancouver Island and the Queen Charlotte Islands and westward into the Gulf of Alaska, suggesting that the whales continue to hug the coast closely except when crossing major waterways such as Dixon Entrance and Queen Charlotte Sound.

TABLE II. Observations of gray whales off British Columbia, 1958–60.

Location and vessel	Date	Remarks
	1957	
Langara Light	Dec. 20–28	Several whales near shore, probably grays

(Table II continued)

Location and vessel	Date	Remarks
	1958	
Langara Light	Feb. 2–30	Several southbound gray whales
Langara Light	Mar. 25–30	10 northbound gray whales and several more blows; mostly April 20–26
Langara Light	June 18, Aug. 20, Sep. 4	3 eastbound gray whales
Langara Light	October	Several gray whales travelling in various directions
Langara Light	Nov. 24	8 blows near shore; 1 gray whale breached
Langara Light	Dec. 2– Jan. 18/59	50+ southbound gray whales
Kains Island Light	Mar. 11– Apr. 12	150+northbound whales; mostly grays
Cape St. James Light	Apr. 12–25	12 gray whales
10 mi east of Cape St. James; *Pacific Ocean*	Apr. 7	8 westbound gray whales
5 mi east of Cape Ball; *Laurier*	Apr. 23	2 gray whales
Princess Royal and Fitz Hugh Sounds	Aug. 1–2	2 gray whales
Off Barkley Sound and Long Beach; *Hillier Queen*	Mar. 14– Apr. 30	Northbound gray whales seen almost every day; mostly April 10–12
2 mi off Pachena Point; *Pacific Ocean*	Mar. 20	10 northbound gray whales
1–2 mi off Amphitrite Point; *Howay*	Apr. 11	12 gray whales feeding
Swiftsure Lightship	Apr. 4–12	28 northbound whales; probably grays
	1959	
Langara Light	May 18	3 eastbound gray whales
Langara Light	Sep. 9	6 southbound gray whales
Langara Light	October, November, December	Many southbound whales, mostly grays; in groups of 4–6
Sydney Inlet; *Pacific Ocean*	June 2	2 gray whales near mouth of inlet
Dixon Entrance	June 20	2 eastbound gray whales
Kains Island Light	Mar. 2– Apr. 1	27 northbound whales, probably grays
Swiftsure Lightship	Apr. 23	3 gray whales
	1960	
Estevan Point to Cape Cook; *Laurier*	Mar. 10–20 Apr. 26	10 gray whales 4 gray whales
Off Long Beach; coastal vessels	Mar. 15–30	Many gray whales
Off Cape Beale; *Atlin Post*	Apr. 3	12 northbound gray whales
Langara Light	Aug. 31	Several gray whales going northwest
Langara Light	September	Many gray whales seen
Langara Light	Sep. 10	6 southbound gray whales; 1 being attacked by killer whales
Langara Light	December	Many southbound gray whales
Langara Light	Jan. 3	Several southbound gray whales

OBSERVATIONS OFF ALASKA

Dr F. H. Fay (personal communication) has kindly supplied the following information on gray whales he has observed in the vicinity of St. Lawrence Island, Alaska. Gray whales, sometimes singly and sometimes in pairs consisting of a mother and a calf, were seen travelling and feeding close to the western shores of St. Lawrence Island from May 11 through July, 1952, from June 4 to July 26, 1953, and from May 11 to June 19, 1954. More recent records from Gambell on the west coast of St. Lawrence Island show that gray whales usually arrive in this area about the middle of May. Dr Fay records the following early arrivals at Gambell: May 17, 1956; May 18, 1957; May 11, 1958; May 20, 1959; and May 21, 1961. Most are seen near the beginning of June but some remain as late as November. Dr Fay records one seen near Northeast Cape, on the west coast, on November 14, 1957, a stranded carcass at Northeast Cape about October 24, 1959, and a fresh stranded carcass near Gambell about October 24, 1959. Most, but not all, gray whales pass along the western shore of St. Lawrence Island on the northward migration; some split off from the main herd and pass northward along the eastern shores of the Island.

Reports from the tug *Neptune* describe whales sighted while running between St. Lawrence Island and Point Barrow in 1958 and 1959. In July, 1959, a school of gray whales followed the vessel into a lagoon located south of Northeast Cape on St. Lawrence Island. During the last two weeks in July, 1958, 8 to 10 whales could be seen blowing at any one time in waters of 8 to 22 fathoms between the Diomedes Islands and St. Lawrence Island. Farther north, in waters of 10 to 20 fathoms, many gray whales were seen feeding 8 to 15 miles from shore between Cape Prince of Wales and Icy Cape. At this time in July, 1958, many unidentified whales were seen from an aircraft flying between St. Lawrence Island and Nome. In August, 1958, a gray whale was observed feeding in water 5 fathoms deep north of Cape Prince of Wales. As this whale surfaced close to the vessel, mud was seen washing from its back.

Mr Karl Kenyon (personal communication) reports that he saw no gray whales while he was hunting walrus at Little Diomede Island in the Bering Straits from May 11 to June 14, 1958. He reports also that he saw no gray whales from Amchitka, located near the western end of the Aleutian Chain, during a year's stay on this island.

A specimen of baleen from a gray whale was taken from the beach on St. Matthew Island on August 4, 1954 (courtesy of Dr Robert Rausch). Gray whales have not previously been recorded from this locality.

MIGRATION ROUTE

The route followed by gray whales in migration between winter breeding and calving grounds in and about the lagoons of Mexico and feeding grounds in the Bering and Chukchi Seas has been the subject of much recent controversy mainly because of insufficient data. Original observations of gray whales off Washington, British Columbia and Alaska presented in this paper are combined, by areas, with selected published records of gray whales from the west coast of North America in the following summary which attemps to define the route and timing of the migration.

MEXICO

Gray whales are concentrated for breeding and calving in coastal areas from San Diego to Cabo San Lucas and the southern end of the Gulf of California, mostly from early January to the end of February; a few stragglers have been seen offshore in the region of Guadalupe and Clarion Islands; some are still present along the Mexico coast in March and April (Gilmore, 1960b). At Magdelena Bay the height of the southward migration is January 22, but early whale catches were made from January 4 to February 16 (Risting, 1928).

CALIFORNIA AND OREGON

The northward spring migration past San Diego begins in mid-February, is at a peak in March and April, and tapers off in early May (Gilmore, 1960b). Five gray whales, one of which was captured, were seen near Crescent City on July 21, 1926 (Howell and Huey, 1930).

Southward migrants arrive along the coast of Oregon and northern California in October and November (Scammon, 1874). Twelve to 15 were seen off southern Oregon in September, 1947 (Gilmore, 1960b).

The southward migration past San Diego occurs from December 25 to February 10, with stragglers passing 3 weeks earlier or later; late southbound migrants overlap early northbound migrants in late February (Gilmore, 1960a).

WASHINGTON AND BRITISH COLUMBIA

The northward spring migration in this locality begins usually in March, is at a peak from mid-March to mid-April, and ends in May.

Stragglers are occasionally seen at various coastal points from the Columbia River mouth to Dixon Entrance and in protected waters of British Columbia during the summer months.

Gray whales are occasionally seen near Dixon Entrance travelling in various directions during fall months; some of these are probably early southward migrants but most appear to linger here throughout the summer and fall.

During periods of good weather in winter many southward migrants pass close to shore in December and January, mostly in late December.

SOUTHEAST ALASKA AND KODIAK ISLAND

There are few records of gray whales from the Gulf of Alaska. One was taken by whalers operating from Baranov Island in southeast Alaska, 3 were taken by whalers off Kodiak, 2 of them in May, 1928 (Gilmore, 1960a). Eight were seen travelling westward along the south coast of Kodiak Island on May 11, 1957 (Wilke and Fiscus, 1961).

ALEUTIAN ISLANDS

No gray whales are seen by Japanese whalers operating north and south of the Aleutian Islands in spring and summer (Ichihara, 1958). The whaling station located at Akutan on Unimak Island recorded no gray whales taken (Kellogg, 1931). A dozen or so were seen passing through Unimak Pass in early June (Turner, 1886) and one was seen in the northern part of Unimak Pass on May 29, 1957 (Ichihara, 1958). No gray whales pass Amchitka in the western Aleutians (Mr Karl Kenyon, personal communication).

BERING SEA FROM ALASKA PENINSULA TO ST. LAWRENCE ISLAND

There are no sight records of gray whales from this region although whalers are active in offshore waters north of the Aleutian Islands throughout late spring, summer, and early fall months. Only once, in July, 1958, have gray whales been seen from the Pribilof Islands (Gilmore, 1960a).

ST. LAWRENCE ISLAND TO BERING STRAIT

Gray whales are well known to residents of St. Lawrence Island where they first appear each year in May (Dr F. H. Fay, personal communication).

Several recent reports show that gray whales, travelling and feeding, are abundant in this area during the summer months. One hundred seventy-two were counted off the northwest coast of the Island on August 2, 1955 (Ichihara, 1958). A school entered a lagoon on the east coast of the Island in July, 1959 (p. 823). Approximately 150 were seen off the east coast of the Island and a scattered few northward to Bering Strait in August, 1958 (Nasu, 1960). Many whales, possibly grays, were seen between the Island and Nome in late July, 1958 (p. 823).

Some gray whales are still found in Bering Strait in October (Nikulin, 1946). Strandings on St. Lawrence Island, mostly along the east coast, occur during fall months as late as November.

CHUKCHI SEA

The Chukchi Sea is closed by ice throughout the spring months and does not open until late June and early July (Maher, 1960). Gray whales are abundant near the arctic Alaska coast during summer months. Many (200+) were seen feeding in Kotzebue Sound on August 10 to 20, 1959, and 20 were seen scattered and moving southward north of Cape Prince of Wales on August 24, 1959 (Wilke and Fiscus, 1961). Eskimos see gray whales migrating northward past Cape Thompson during the first half of July each year (Fay, MS, 1961a). Many whales, some of which were definitely grays, were seen feeding off Kotzebue Sound in July, 1958 (p. 823).

Maher (1961) provides the following information: 9 gray whales were taken by Eskimos between Wainright and Point Barrow from July 18 to September 13, 1954 to 1959; 50 to 100, travelling southward, were seen from the beach at Wainwright on August 9 to 10, 1953; a few were seen passing Cape Sabine on August 3 to 5, 1959; gray whales are scarce at Point Barrow; gray whales are present near Point Barrow until mid-September, but some may begin moving southward in early August.

Gray whales are also abundant near the northern Siberian coast during early summer until ice restricts their movements. Seventy-eight were seen from a Japanese oceanographic vessel off the Siberian coast on July 27, 1958 (Nasu, 1960). Fifty-eight were taken by Japanese whalers off the Siberian coast in August, 1940 (Mizue, 1951).

KORYAK COAST

Gray whales arrive off this coast in May and early June; they no longer range southward to Kamchatka (Sleptsov, 1955). Thirty-one gray whales were taken by the "Vega" expedition between Cape Olyutorskii and Cape Navarin from July 27 to August 19, 1925 (Risting, 1928). A few were seen off the Gulf of Anadyr in August, 1958 (Nasu, 1960).

Two major gaps remain in our knowledge of the route followed by this population of gray whales. Knowledge of the route between British Columbia and feeding grounds in the Bering Sea during both northward and southward migrations remains speculative. Available evidence as to the most probable route taken will be discussed later.

Northward migrants pass San Diego from February (when others are still moving southward) into May, but mostly in March and April. The literature contains no information on the exact dates during which peak numbers pass by this point going north. Near Cape Flattery, some 1200 miles north, peak numbers pass during the first two weeks in April. The peak of the northward migration past San Diego is, therefore, probably within the first two weeks of March, assuming a rate of travel of 35 to 50 miles per day or 1.5 to 2.0 knots. From San Diego the whales appear to head directly across the Santa Catalina bight and are several miles from shore when passing La Jolla (Gilmore, 1960b). Farther north they travel close to shore, skirting headlands and usually cutting directly across the mouths of large bays.

The re-appearance of gray whales on the southward run off San Diego begins in early December and ends in late February; most whales pass during the middle two weeks in January (Gilmore, 1960b), at which time they are travelling in a narrow stream, little more than a mile wide, at an average rate of 4.6 knots, and seem to converge on the kelp beds off La Jolla (Wyrick, 1954). Similarly, at San Simeon, located on a coastal bight, pregnant females appear closer to shore during the "down" season as they seek bays and lagoons to bring forth their young (Townsend, 1886). Scammon (1874) states that they appear off the coast of Oregon and northern California during October and November and that both males and females keep near to shore during the southward passage. Observations off northern British Columbia show that, although gray whales appear during the fall months, the main herd of southward migrants does not pass until December and January, with maximum numbers passing in December. Off the north end of Vancouver Island they pass in greatest numbers near the end of December and off Washington in early January. The southward run from British Columbia to San Diego appears to take from 2 to 4 weeks at an average rate of about 50 to 100 miles per day or 2 to 4 knots.

The southward migrants proceeding towards the breeding grounds are more concentrated, pass by over a shorter period of time, and travel at a faster rate, than the northward migrants proceeding towards the feeding grounds (Fig. 2).

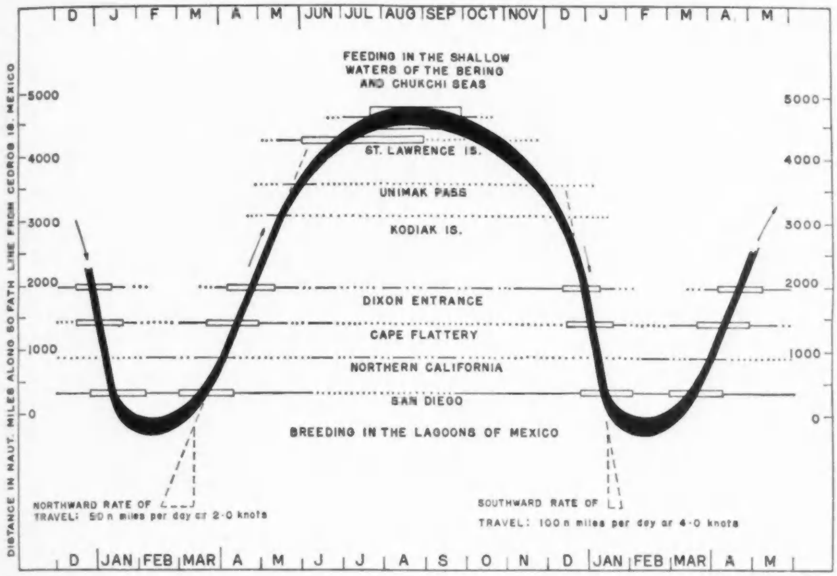

FIG. 2. Diagram summarizing the seasonal distribution of the American herd of gray whales. Relative abundance is indicated horizontally across the graph as follows: *open rectangles*—numerous; *solid line*—few records; *dotted line*—probable occurrence.

The route from Dixon Entrance to the Bering Sea is unknown except for a few observations of westbound whales from the south coast of Kodiak Island in May (Wilke and Fiscus, 1961) and north of Unimak Pass in late May and early June (Ichihara, 1958; Turner, 1886). None have been reported by oceanographic and fisheries research vessels operating offshore in the Gulf of Alaska and none have been reported by Japanese whalers operating north and south of the Aleutian Islands. The *Baikal Maru* operated from 48° to 54°N and 159° to 173°W from May 20 to October 3, 1953, and saw no gray whales (Sakiura and Ozaki, 1953). We consider that this evidence, although negative, is important in showing that gray whales do not cross the Gulf of Alaska on leaving British Columbia, but continue to follow the coastline northward and westward towards Unimak Pass. The coastal route is approximately 200 miles greater than a direct route across the Gulf, and would, therefore, not greatly prolong the journey.

Japanese whalers operating in the Bering Sea concentrate their hunting in areas which lie to the west of a line joining Unimak Pass and St. Lawrence Island, in waters outside the 50-metre contour (Fig. 3). Whaling is conducted from June to September, but no gray whales are seen. Gray whales have only once been reported from the Pribilof Islands, which also lie to the west of this line. Fiscus saw 3 or 4 gray whales off St. Paul Island on July 2, 1958 (Gilmore, 1960a). Gray whales have never been reported from the Aleutian Islands west of Unimak Pass. We consider that this evidence strongly favours a route which crosses the Bering Sea in its eastern part over the Alaskan continental shelf rather than in the western part as suggested by Gilmore (1955, 1960a, 1960b) At St. Lawrence Island gray whales first appear off the east coast in May, following the retreat of the pack ice. Whaling statistics show that they appear along the Koryak coast first in July (Risting, 1928) although the area is ice-free in June. The earlier arrival of gray whales off St. Lawrence Island suggests that the route followed is by way of the eastern rather than the western Bering Sea.

Fay (MS, 1961a), records 13 strandings of gray whales on St. Lawrence Island, where the species is occasionally hunted by the Eskimos, from 1955 to 1959. Most of these occurred in July and August; the latest stranding was in October. About two-thirds of the stranded whales were young animals less than 30 feet (9.2 m) in length, and 2 had been injured by killer whales. Three gray whales, each carrying crude harpoons of a type used by the natives of Cape Chaplin, stranded on St. Lawrence Island in September, 1961.

Three strandings on the Alaska mainland in 1959 are recorded by Fay (MS, 1961a). One stranded on September 4 at Scammon Bay, south of Norton Sound, where Eskimos report the species to be rare. Two stranded in August near Cape Thompson, 125 miles northwest of Kotzebue, where Eskimos report gray whales migrating northward during the first half of July each year.

A map showing the distribution of the American herd of gray whales is presented in Fig. 3. Arrows indicating the route past St. Lawrence Island represent probable routes taken by the main herd. Some whales pass northward along the east coast of the Island and, no doubt, some also pass southward along the west side.

The northward migration in June and July is impeded by the retreating pack ice which, in most years, provides a lead past the west coast of St. Lawrence Island in early June and through Bering Strait in July. Maher (1960) shows the approximate mean limits of the pack ice at about 300 miles north of Bering Straits in the Chukchi Sea, in August and September. Ice re-appears in the Gulf of Anadyr and closes Bering Strait in October. It then moves rapidly southward until December when it completely closes the northern part of the Bering Sea from Cape Navarin to Nunivak Island.

Leads past St. Lawrence Island are closed in December or January. Assuming a rate of travel of 50 to 100 miles per day (2 to 4 knots) gray whales would cover the 2000-mile distance between St. Lawrence Island and Dixon Entrance via Unimak Pass in 3 to 6 weeks. Most gray whales pass northern British Columbia in December, which suggests, on the basis of the foregoing assumptions, that most of the herd leaves the Bering Sea early in November. A few southward migrants (which had probably left the Bering Sea in September and October) are seen off northern British Columbia in October and November.

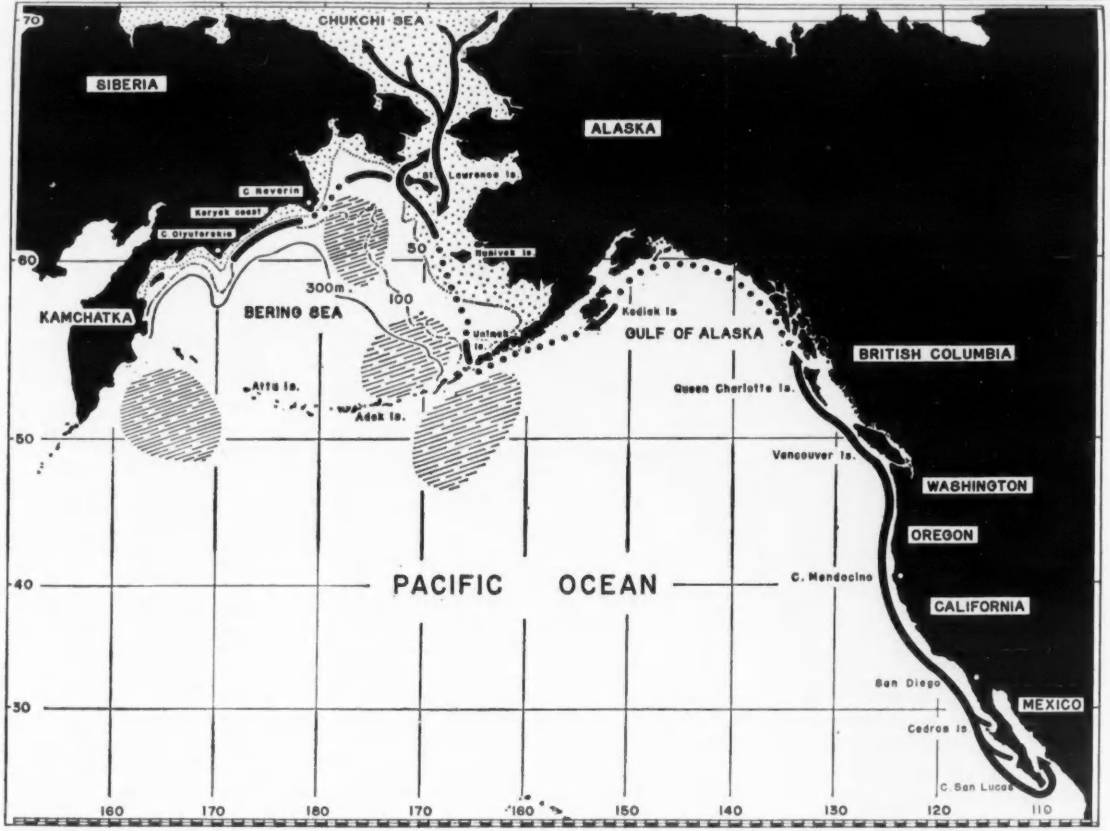
CHUKCHI SEA
SIBERIA
ALASKA
St Lawrence Is
C Navarin
Koryak coast
C Olyutorskie
Nunivak Is
50
300m
100
KAMCHATKA
BERING SEA
Unimak Is.
Kodiak Is
GULF OF ALASKA
BRITISH COLUMBIA
Queen Charlotte Is.
Attu Is.
Adak Is.
Vancouver Is.
WASHINGTON
OREGON
PACIFIC OCEAN
C. Mendocino
CALIFORNIA
San Diego
MEXICO
Cedros Is
C. San Lucas
70
60
50
40
30
160
170
180
170
160
150
140
130
120
110

FIG. 3. Map showing the distribution of the American herd of gray whales. Solid lines: known routes; broken lines: probable routes; hatched areas: commercial whaling areas where gray whales are not seen.

TABLE III. Distances from Cedros Island, Mexico, along the migration route of gray whales.

Location	Distance in nautical miles	
	Point to point	Cumulative
Cedros Island	0	. . .
San Diego	300	300
Point Conception	240	540
Cape Mendocino	420	960
Cape Flattery	500	1460
Cape Scott	200	1660
Cape St. James	120	1780
Langara Island	180	1960
Unimak Pass	1600[a] (coastal)	3560
St. Lawrence Island	700[b] (direct)	4260
Koryak Coast, Siberian Coast or Point Barrow	400–600	4660–4860

[a]Direct distance across the Gulf of Alaska is approximately 1400 miles.

[b]Approximate distance along Aleutian Islands to St. Lawrence Island is 2000 miles via Attu and 1400 miles via Adak.

FEEDING

A sample from the stomach contents of 2 small gray whales taken near Gambell, west coast of St. Lawrence Island, were as follows:

(1) Taken June 9, 1954; sample size about 200 cc

Amphipods: several *Ampelisca macrocephala*; one *Anonyx nugax*
Polychaetes: several tubes of *Pectinaria* (sp.)
Gastropods: one moon-snail, family Photidae
Other: some sand and silt

(2) Taken May 29, 1958; sample size about 1 litre

Amphipods: about 90%; mostly *Ampelisca eschrichti*, few *Anonyx nugax*
Ascidians: remains of 2 compound, branched and globular ascidians
Decapods: 2 intact spider crabs, *Chionoecetes bairdi* and *Hyas coarctatus*
Lamellibranchs: remains of 3 small bivalves; one 7-mm shell of *Liocyma*, probably *L. fluctuosa*
Polychaetes: 2 pieces of shells from *Pectinaria*
Cumacea: remains of 1 unidentified specimen
Gastropods: a 9-mm shell of *Volutina*; part of an operculum
Other: some sand and a few bits of wood

Tomilin (1954) earlier described gray whales in arctic regions as feeding upon near-benthic amphipods and true benthic organisms, including polychaetes, hydroid polyps, the mollusc *Buccinum*, and others, in some cases mixed with tiny pebbles and silt.

Feeding behaviour of gray whales in shallow waters has been described by several authors. Scammon (1874) describes gray whales surfacing with head and lips besmeared with mud from soft bottoms. Wilke and Fiscus (1961) describe gray whales feeding in August in the Chukchi Sea, in waters of about 24 fathoms, making muddy blotches in the water as they surfaced, apparently having expelled the mud through the baleen. Tomilin (1954) describes the baleen plates of the gray whale according to the animal's ability to dig up and probably even plough up the silty benthic ground. Reports of the tug *Neptune* describe gray whales surfacing with mud washing from their backs as they fed in water 5 fathoms (9 m) deep north of Cape Prince of Wales in August. Seabirds have been seen following feeding gray whales and settling into the muddy spots where the whales had surfaced (Wilke and Fiscus, 1961).

Fay (MS, 1961a) describes the waters about St. Lawrence Island as an important summer feeding ground. Here gray whales feed usually in waters of 15 fathoms (27 m) or less and within 300 yards (270 m) of shore, creating muddy patches in the water as they surface. Photographs taken by Dr Fay show them feeding in the surf within 50 feet (15 m) of the beach (Fig. 4).

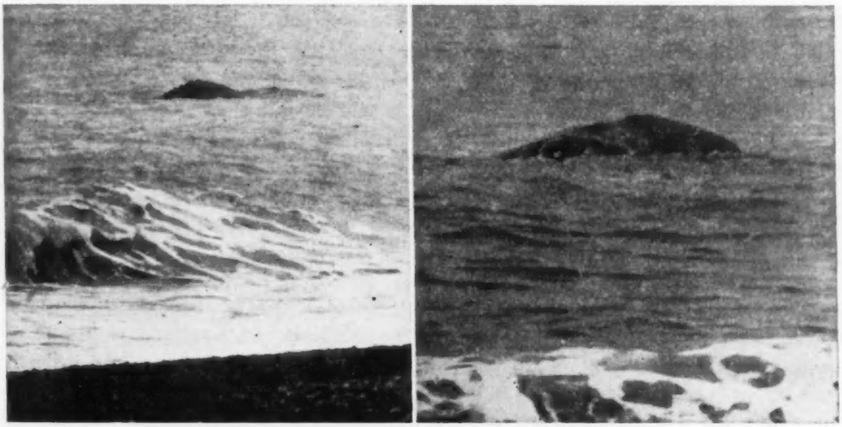

Fig. 4. Gray whales feeding close to shore off St. Lawrence Island, Alaska. (Photo by Dr F. H. Fay.)

Outside its arctic habitat, gray whales appear to feed little (Andrews, 1914; Townsend, 1886; Scammon, 1874). Scammon (1874) observed that stomachs of gray whales caught in the breeding lagoons were usually empty although some contained "sedge" or "sea-moss". He also describes mussels found in the mouths and among the baleen, but does not state the locality in which this occurred. Matthews (1932) describes sei, humpback and gray whales feeding on schools of the anomuran decapod *Pleuronocodes planipes* in Magdelena Bay, in 1926. Dr Carl L. Hubbs (personal communication) relates local testimony that "several barrels of sardines" were found in the stomach of a gray whale stranded near the north end of San Ignacio Lagoon in Mexico. Mizue (1951) reports that the anomuran decapod *Nephrops thomsoni* was found in the stomachs of 2 gray whales caught in the northern waters of the Yellow Sea in May 1922.

Two reports suggest that gray whales injest plant material incidentally during bottom forages while on migration. Andrews (1914) examined a number of stomachs of gray whales during the southward migration off North Korea and found only dark green water with bits of kelp, seaweed and a light gelatinous material he thought might be jelly-fish. The present author examined the stomachs of 10 gray whales taken under special permit by whale catchers off the west coast of Vancouver Island, near the mouth of Quatsino Sound, in April, 1953, during the northward migration. These stomachs contained a green liquid within which was suspended bits of plant material; the intestines contained variable quantities of thick mucous coloured from a dark cream to a yellow-green. Although these stomachs contained no animal material, the cream-coloured intestinal contents suggest animal material in an advanced stage of digestion and that the whales had probably been feeding. Mizue (1951) reports only green-coloured gastric juice in the stomachs of gray whales taken during the southward migration off Korea.

Observations off Washington and British Columbia during the northward migration in March and April show that gray whales occasionally tarry to feed en route. Behaviour which is described as feeding has been reported from several localities along the coast of Washington and Vancouver Island, but mostly from the Umatilla Lightship and along Long Beach. The depth of water at Umatilla is 20 to 25 fathoms (37–46 m) over a sandy bottom; the depth where whales feed along Long Beach is 5 to 10 fathoms (9–18 m) over a sandy bottom. The overall rate of progress north of San Diego appears to be slower during the northward run, probably as a result of frequent interruptions in the migration as the whales slow down or stop for the purpose of resting or feeding.

Dr Carl L. Hubbs (personal communication) cites instances of gray whales near La Jolla stopping sometimes for more than an hour, circling tightly, and otherwise behaving as though feeding, while most whales carry on without hestitation; in one specific instance gray whales behaved in this manner on the occasion of the spawning of squid off La Jolla, on January 21, 1954.

Howell and Huey (1930) report that a male gray whale, 39 feet or 11.9 m long, in company with 4 others, was taken by whale catchers off northern California in July, 1926. This whale had within its mouth and among its baleen a quantity of *Euphausia pacifica*.

DISCUSSION

Original observations described in this paper, when combined with recent publications on the species, show that gray whales follow the coastline closely when migrating between the breeding lagoons of Mexico and the northern part of British Columbia, and that they stop on occasion to rest and to feed. The northward migration is more protracted in time, proceeding at a slower rate than the southward migration. Information on the migration route north of British Columbia is scanty. Lack of offshore sightings in the Gulf of Alaska, combined with a few sightings along the coast, however, suggest that northward migrants continue to hug the coastline while circumscribing this area. Similar evidence along the Aleutian Chain and in the Bering Sea suggests that during the northward run, gray whales pass through Unimak Pass and/or Isanotski Strait and proceed directly towards the west coast of St. Lawrence Island. Off the west coast of St. Lawrence Island gray whales begin to disperse as they search for food. Some disperse westwards to feed off the Koryak coast and the Gulf of Anadyr; some proceed northward past St. Lawrence Island following the retreat of the ice through Bering Strait in July. The migration route splits again north of Bering Strait with some whales following the Siberian coast in a northwesterly direction and some continuing northward across the mouth of Kotzebue Sound to follow the Alaska coast northwesterly towards Point Barrow.

Open ice-free water permits feeding in the Chukchi Sea during July, August and September. From August to September, with the encroachment of ice through Bering Strait, gray whales proceed southward usually, past the east coast of St. Lawrence Island. They are next seen, travelling close to shore, along the coast of British Columbia, mostly in December and January. Some, probably those which fail to complete the migration to its limits in the Bering and Chukchi Seas, are present along the northern British Columbia coast as early as September, others spend the summer between northern California and southeastern Alaska.

The scarcity of reports of gray whales from whalers and from research vessels operating in oceanic regions off British Columbia, in the Gulf of Alaska, north and south of the Aleutian Islands, off Kamchatka, and over deep waters of the central and western parts of the Bering Sea is, in my opinion, convincing evidence that gray whales avoid these areas during migration and feeding. The absence of reports of gray whales in coastal regions such as Unimak Pass and the southeastern coast of Alaska, however, is not convincing evidence that gray whales avoid these localities. Experience has shown that gray whales travelling close to shore are difficult to see against the breaking surf by vessels which must keep well off shore along treacherous storm-lashed and rock-strewn coasts.

Existing knowledge of ocean currents and of whale migrations fails to support the theory (Gilmore, 1955, 1960a, 1960b) that gray whales follow ocean currents. Previous attempts to relate oceanic migrations of other whale species to ocean currents have been unsuccessful (Harmer, 1931; Townsend, 1935; Dawbin, 1956). With few exceptions, gray whales, wherever observed, have been travelling close to shore where large oceanic water masses lose their identity under the influence of topographical irregularities in the coastline, freshwater run-off, and climatic aberrations caused by proximity to land. One of several inconsistencies in Gimore's theory that gray whales are assisted in their migration by ocean currents is that the coastal Davidson Current flows northward along the North American coast to at least 48°N Latitude in November, December and January (Sverdrup *et al.*, 1946) at a time when migrating gray whales are travelling southward. Another inconsistency is that there is no appreciable surface current northward of the Strait of Juan de Fuca to Dixon Entrance in summer (Favorite, 1961) as gray whales migrate northward. The effects of local run-off, which can be traced several hundred miles offshore along the coasts of British Columbia and Washington (Favorite, 1961), show no evidence of deflecting gray whales in their migration.

In seeking environmental conditions associated with the distribution of gray whales, it would be more appropriate to consider the coastal climate and topography rather than the oceanic climate. A continuous temperate faunistic province stretches along the west coast of North America from the middle of lower California, along the coastal arch to the Aleutian Islands, and continues uninterrupted in the eastern Bering Sea as far north as the Bering Strait (Ekman, 1953). The Aleutian Trench and the basin of the western Bering Sea constitute faunistic barriers. Coastal waters of the Asian parts of the Bering Sea, the sea around Kamchatka, and the Okhotsk Sea are distinctly Arctic. The American side of the Bering Sea is, however, warmed by northward-flowing temperate water which is seldom less than 6°C even in July and August. Bottom topography of the Bering Sea features a wide continental shelf in its eastern parts. The 50-metre contour continues through Unimak Pass to outline a narrow band along the north side of the Alaska Peninsula, curving into Bristol Bay and continuing in a northwest direction to the west coast of St. Lawrence Island. Bering Strait and the Chukchi Sea are mostly less than 30 m in depth.

Ichihara (1958) admits doubt as to the true migration route of the gray whale in the Bering Sea, but draws inferences from the migrations of other baleen whales in this area as learned from marking experiments. There is, however, little reason to expect gray whales, which are known to hug the coastline closely during a large part of their migration, to conform to migration routes used by other whale species which are oceanic in their distribution; nor should we expect them to select feeding areas used by other whales. Hardy and Gunther (1935) and Nemoto (1959) have shown that oceanic species of baleen whales concentrate in feeding areas as an indirect result of the search for preferred foods. Euphausians are a preferred food of fin and humpback whales whose feeding apparatus is adapted to skimming these as they swarm near the surface, usually off the edge of the continental shelf or in areas of convergences. Only one euphausiid, *Thysanoessa raschii*, is abundantly distributed in cold shallow waters of the Gulf of Anadyr and the northern Bering, Chukchi and Okhotsk Seas. Fin and humpback whales may feed directly or indirectly on this species in shallow waters in the northern parts of the Bering Sea (Nemoto, 1959) where they are sometimes associated with gray whales, but mostly these whales concentrate along the edges of the shelf in deeper waters. The gray whale, however, is adapted to feeding on benthic or near-benthic organisms (Tomilin, 1954) which abound in cold shallow seas. It would neither be expected to distribute itself in the same manner as those whales which feed on epipelagic plankton, nor does evidence from stomachs and feeding behaviour indicate that it does.

There is no evidence available to show that gray whales ever cross broad expanses of ocean or stray far from land. Throughout the feeding migration south of the Bering Sea, they travel in a general northwesterly direction, keeping exposed ocean coasts of all major land masses, including large islands such as Vancouver Island, the Queen Charlotte Islands and Kodiak Island on the right side. When passing small islands such as Solander Island, where an unobstructed view of open ocean appears beyond, they pass on the inside; when passing large islands where an unobstructed view of open ocean does not appear, they pass on the seaward side.

The combination of senses providing clues to the migration route is not certain. Circumstantial evidence suggests that gray whales supplement their directional sense by means of visual clues provided by coastal landmarks. In this regard, Gilmore (1960a) remarks on the gray whale's habit of periodically thrusting its head out of the water, while subsequent movements suggest re-orientation, and on page 417 of his paper he illustrates this behaviour with the caption "gray whale spying out a boat". Scammon (1874, p. 32) illustrates similar behaviour of gray whales in the Arctic ice. While blowing, the gray whale barely exposes the eyes.

The distance (d) in nautical miles at which landmarks of various heights (h) in feet may be seen from the sea surface is described by the formula:

$$d = 1.2\sqrt{h}$$

According to this formula, landmarks 100, 500, 1000, 2000, 4000 and 8000 feet high are visible from approximate distances of 10, 25, 35, 50, 75 and 100 nautical miles, respectively (1 foot = 0.305 m). Although it is not certain that baleen whales in general and gray whales in particular are anatomically equipped to see great distances in air (some authorities generalize that the Mysticetes lack the power of accommodation and are myopic in aerial vision), their behaviour in following the coastline, except when by-passing wide openings in the coastline, suggests that they are utilizing landmarks for orientation. High mountains fringing the west coast of North America provide an almost continuous path for gray whales should they utilize these for directing their coastal courses between breeding and feeding areas. Specific mention has been made of one locality where gray whales appear temporarily to deviate from their route. This is the mouth of Queen Charlotte Sound, a gap of 120 miles between Cape Scott and Cape St. James. Mountains near the southern end of Queen Charlotte Islands range to heights of from 1500 to 2000 feet (460–610 m) and could not be seen from the sea surface at distances greater than 40 to 50 miles. Northbound whales appear to continue on a northwesterly course after leaving Vancouver Island; later, probably when within sight of these mountains, they appear to re-orientate in the direction of Cape St. James. Some may continue northward through Hecate Strait. Future studies in Queen Charlotte Sound are planned in order to learn how gray whales orient themselves in the absence of visible landmarks.

Navigational aids used by gray whales need not be completely innate since calves accompany their mothers on their first northward migration, and are thereby provided with the opportunity to learn the route.

SUMMARY AND CONCLUSIONS

The northward migration of gray whales along the coasts of Washington and British Columbia begins in February, ends in May, and is at a peak during the first two weeks in April. At the peak of the migration, gray whales are seen almost every day at several points between the Columbia River and Dixon Entrance, travelling close to shore except when by-passing wide indentations in the coastline at which time they travel from headland to headland. None are seen offshore. Occasional stops are made for resting and feeding.

Few southbound migrants are seen off Washington and British Columbia because of reduced visibility in winter months. The southward migration begins in late September and October, ends in late January, and is at a peak in late December. Gray whales continue to hug the coast on the southward run, but appear to be travelling at a faster rate and seldom stop to rest or feed.

Gray whales sometimes occur along the coast and in protected waters of British Columbia from June through September. At this time the direction of travel is not constant; these whales are probably summer residents in the area and are not migrating.

On their feeding grounds in the Bering and Chukchi Seas, gray whales feed on benthic and near-benthic organisms, mostly amphipods. They are, consequently, distributed over the shallow continental shelf in northern regions rather than in offshore oceanic areas where commercial species of baleen whales distribute themselves in search of favoured epipelagic plankton. When dispersing to feed, gray whales first appear off the west coast of St. Lawrence Island in May. The herd splits up in this region with part travelling westward towards the Koryak coast and part continuing northward through Bering Strait. The herd splits again in the Chukchi Sea with part travelling westward along the Siberian coast and part travelling northward along the Alaskan coast. Encroachment of the ice through Bering Strait in October probably initiates the southward migration which is directed mainly along the eastern side of St. Lawrence Island.

Available evidence suggests that northward migrants travel a coastal route until they reach the western tip of the Aleutian Peninsula where they enter the Bering Sea and continue northward within the 50-metre contour which outlines a broad pathway in the eastern Bering Sea. It is unlikely that they follow ocean currents, since throughout known parts of the migration they travel close to shore where ocean currents lose their identity under the influence of coastal configurations.

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Air Blowing of Cod Liver Oil and Other Marine Oils[1]

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ABSTRACT

The polymerization of cod liver oil by blowing with air was investigated at temperatures ranging from 80 to 140°C. The changes occurring in the chemical and physical constants were plotted and the effects of reaction variables studied. Polymerization of herring oil and seal oil was compared with cod liver oil under the same conditions. The use of these blown oils as possible additives to lubricating oils is suggested.

INTRODUCTION

Blown oils have been used extensively for many years as additives to lubricating oils, as drying oils in paints, and for some other purposes. Their use in lubrication goes back almost a century, but with the introduction of mineral oil lubricants, blown oils assumed a minor role as additives to certain specialty lubricants. These blown oils must therefore be completely miscible with mineral oils and no settling out should occur from a 10 to 20% solution in mineral oil. The acidity expressed as percentage free fatty acids (FFA) should be low and 3 to 5% is usually given as the maximum allowed. The colour must be uniform from batch to batch and the viscosity would have to be within close tolerances according to lubricating oil manufacturers' specifications. The iodine value must be low to avoid "skimming over" on storage and to avoid oxidation when hot.

In Canada today only blown rapeseed oil is used in any volume by the major lubricating oil companies. The purpose of this study was to determine if a blown oil could be prepared from marine oils to meet the specifications set by the oil companies. Since cod liver oil can now be obtained at prices approaching those of other industrial marine oils, this oil was chosen for study despite its high iodine value. Seal oil and herring oil were also studied and found to behave similarly to cod liver oil when blown.

In industrial practice, the oil is processed in a tall cylindrical vessel supplied with coils for heating and cooling, while air from a blower is bubbled through the oil from perforated pipes near the bottom of the tank. Steam is first circulated through the coils to bring the temperature up to 90–100°(C), but the oxidation process soon causes the temperature to rise further and cooling water must then be circulated through the coils. The temperature is usually allowed to rise to 120–130° (Archbutt and Deeley, 1927) and the blowing continued until the desired viscosity is reached. If the temperature is allowed to rise still

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higher, excessive darkening occurs. The specific gravity increases, finally ranging from 0.96 to 0.99 in a typical oil blown for lubrication. Some decomposition occurs with liberation of volatile compounds having an obnoxious odour, and the iodine value drops rapidly especially at higher temperatures but gradually levels off as the viscosity increases. The FFA content of the oil also increases although many of the short-chain acids are blown off.

Bailey (1952, p. 302) lists a number of patents for preparing polymerized fish oils other than blown oils for use in blended lubricants. Kumagai (1931) first hydrogenated the oil to an iodine value between 120 and 150 and then catalytically polymerized it. Toyama and Ishikawa (1933) describe a process whereby the oil is cold cleared at 0°, polymerized at 250 to 300° in the absence of air and then steamed. According to Wasson (1938), 0.01 to 0.05% sulphur, selenium or tellurium may be added to a polymerized oil such as fish oil to serve as a stabilizer.

Catalysts for the polymerization of oils are the subject of numerous patents. Eichwald (1939) and Whiteley and Turner (1941) described the use of boron trifluoride while Noack and Dunbar (1953) found that sulphur dioxide was a rapid heat-bodying catalyst in blowing oils. I. G. Farbenindustrie A/G (1937) and Behr (1941) listed selective solvents that can be used to extract relatively saturated unpolymerized portions from the polymerized oils.

In the marine oils field, Thomson and Ballantyne as early as 1892 described the blowing of sperm oil for lubricating purposes and tabulated the properties of the blown oils. Thomson (1926) tabulated the changes in shark, sperm and whale oils during blowing under varying conditions.

Several authors have investigated the blowing of marine oils with their use as drying oils in paints as the primary objective. Brocklesby and Denstedt (1934) studied the blowing of pilchard oil at the rather high temperature of 250° and reported that the iodine value dropped to 80 from 180 in 21 hr. The FFA content levelled off at approximately 3% since most of the short-chain acids formed, such as acetic and propionic, would be blown off at this temperature. O'Hare and Withrow (1947) oxidized sardine oil at 105° by air blowing and plotted the chemical and physical changes which occurred during oxidation. Bittenbender (1950) reported on the experimental production of blown menhaden oil using temperatures from 58 to 111°, blowing with air or oxygen, and on the use of certain additives, chiefly peroxides. The effects of air flow, agitation and temperature on the polymerization of vegetable drying oils were reported by Hess and O'Hare (1950, 1951). Taylor (1950) and Balbi (1952) have published reviews on the practice of blowing.

The chemical changes taking place in fatty oils during oxidative polymerization are very complex and depend on the conditions used. Carriere (1947) and Privett (1959) have reviewed the latest theories on the subject. Gillam (1949) divided the oxidized products of unsaturated fatty oils into four types, each associated with one temperature range and claimed: Type I products are hydroperoxides formed at room temperature with no change of unsaturation; Type II products, such as oils blown at 100 to 120°, contain a maximum of peroxides formed by direct attack at the double bond, molecular growth being largely by esterification of fatty acids with hydroxyl groups; Type III products (oils blown at 150 to 200°) are initially activated by oxygen, but the products formed are unstable and molecular growth gives acetone-insoluble polymers; Type IV products (oxidation above 200°) polymerize by conjugation and ring formation but initial activation by oxygen still forms part of the reaction.

Perkins and Kummerow (1959) and Firestone *et al.*, (1961) isolated several polymer fractions from cottonseed oil oxidized at 200 to 225° and found that the remaining unsaturation was very difficult to hydrogenate. This explains why the iodine value of a blown oil cannot be brought down below a certain value, dependent on the iodine value of the starting material. In Canada, Sims (1956) has made extensive studies of the heat polymerization of vegetable oils. Cyclic monomers have been isolated from polymerized oils (McInnes *et al.*, 1961) but only circumstantial evidence exists for the presence of these compounds in blown oils.

EXPERIMENTAL

The cod liver oil was supplied by courtesy of Fishery Products Limited, St. John's, Nfld.; the seal oil was rendered from harp seals (*Phoca groenlandica*) and was supplied by courtesy of Karl Karlsen and Company Limited, Halifax, N.S., and the herring oil was a commercial oil produced in British Columbia. The physical and chemical constants of these oils are listed in Table I.

TABLE I. Physical and chemical constants of (marine) oils studied.

	Cod liver oil	Seal oil	Herring oil
Iodine value	168	146	135
Free fatty acids, %	0.8	0.5	1.4
Unsaponifiable material, %	1.5	0.3	1.0
Colour, Gardner	4	3	6
Viscosity, Gardner, 25°C	A	A	A
Viscosity, stokes, 25°C	0.5	0.5	0.5
Saponification value, mg KOH/g	185	192	190
Refractive index, 25°C	1.47744	1.47478	1.47362
Stearine	Clear at 2°C	Almost solid at 2°C	Almost solid at 2°C

Each batch consisted of 1500 g oil and was blown in a heavy glass tube, 7 cm inside diameter and 75 cm deep. The air was taken from the laboratory supply of compressed air, passed through a Fisher and Porter Flowrator, Series 700 Rotameter, and was dispersed in the oil at the bottom of the tube through a sintered glass plate 3 cm in diameter. The oil was heated by a fibreglass heating tape wrapped around the tube and power input was controlled by a Variac transformer. A thermocouple was immersed in the oil, and a constant record of the temperature was kept on a Leeds and Northrup Speedomax recorder. Very little heat was given off during the oxidation, so cooling was not necessary. In industrial practice it would be necessary to circulate cooling water through the

TABLE II. Physical and chemical constants of blown oils.

Run No.	Type of oil	Time blown	Catalyst	Air flow	Temp.	Iodine value	FFA	Refractive index	Viscosity Gardner	Viscosity (stokes)	Colour Gardner	Remarks
		hours		*ml/min*	°*C*		%	25°	25°	25°		
6	Cod liver	100.5	None	1600	100	101.6	2.6	1.48498	Z–1.8	34.7	14	...
5	"	71.5	"	"	130	100.0	1.7	1.48658	Z–3	46.3	16	...
7	"	73.5	"	4800	100	91.4	3.4	1.48518	Z–5.7	133.2	13	...
12	"	49	"	6500	80	96.8	4.7	1.48447	Z–4.7	88.0	10	...
10	"	41.5	"	"	100	86.2	4.9	1.48518	>Z–6	>148.	13	...
17	"	24	"	"	110	83.1	4.9	1.48442	Z–5.4	118.3	12	...
18	"	23	"	"	120	81.5	4.1	1.48503	>Z–6	>148	14	...
21	"	23.5	"	"	130	78.8	4.7	...	>Z–6	>148	...	...
23	"	6.25	"	"	140	99.6	3.1	1.48361	X+0.5	15.3	14	...
24	"	7	"	9500	130	98.5	3.6	1.48346	X+0.6	22.7	12	...
9	"	62	0.025% BF_3	4800	100	87.5	5.1	1.48558	>Z–6	>148	13	...
8	"	49.5	0.5% BF_3	"	"	93.0	4.9	1.48558	Z–5	98.5	16	...
11	"	26	0.025% BF_3	6500	"	96.5	3.9	1.48452	Z–4	63.4	12	...
13	"	29.5	0.004% Ca	"	"	90.8	4.8	1.48412	Z–4.3	73.9	11	...
15	"	48	0.0133% Ca	"	"	91.0	4.4	1.48473	Z–5.1	103.5	13	...
14	"	28.5	0.013% Co	"	"	98.8	2.0	1.48643	>Z–6	>148	15	...
16*	Alkali-refined cod liver	30	None	6500	100	92.5	4.2	1.48372	Z–4	63.4	11	...
19	Seal	28	"	"	"	79.7	6.7	1.48051	Z–2.7	43.3	10	...
20	Herring	29	"	"	"	64.5	7.6	1.47990	Z–4	63.4	11	...
22	Cod liver	7	"	"	130	103.7	3.5	1.48311	W	10.7	13	Glycerol added
25	"	7.5	"	9500	"	99.8	3.1	1.48326	×+0.5	15.3	12	Steamed
26	"	8	"	"	"	99.8	3.2	1.48321	Y	17.6	13	Steamed

*The free fatty acid content of the alkali-refined oil was 0.2%.

coils during the period of most vigorous reaction. Due to variation in line voltage a certain fluctuation in temperature was experienced but the average deviation in most runs was in the range of 1 to 3 Centigrade degrees.

The iodine value and FFA determinations on the products were carried out according to the American Oil Chemists' Society Official and Tentative Methods (1946). The viscosity was determined using a Gardner Bubble Viscometer, Varnish Series A to T, and Heavy Bodied Series U to Z-6 at 25° and the values obtained were converted to stokes. The colours were compared with Gardner's Colour Standards. The refractive indices were measured on a Bausch and Lomb precision refractometer.

The metallic catalysts used were Calcium 4–78 (4%) and Cobalt (6%) driers manufactured by Nuodex Products of Canada, Ltd. Boron trifluoride was added in the form of the etherate which was prepared according to Laubengayer and Finlay (1943).

The settling tests were carried out as a 10% solution of blown oil in Imperial Oil LCT 20 lubricating oil.

The hydroxyl values were determined by phthalation according to Verbeck (1949), and the near-infrared spectra with a Beckman DK-2 spectrophotometer on samples dissolved in carbon tetrachloride.

RESULTS AND DISCUSSION

In Table II the results of various runs are tabulated. These results would be of only limited use to an industry starting an operation of this type, due to variations in blowing vessel, air distribution, heat transfer and other factors. However, by plotting the constants from a few test runs against blowing time or temperature, these data should provide a guide to the viscosity, iodine value and colour of the product to be expected.

IODINE VALUE

In Fig. 1, the change in iodine value vs. blowing time is plotted for several temperatures at constant air-input rate. The lowest iodine value obtained using this particular cod liver oil was 79, but the product was then practically a solid gel. One specification for blown rapeseed oil is an iodine value of 70, but additional treatment would be necessary to bring the iodine value of cod liver oil down to this level. Marine oils of low iodine value, e.g. seal oil and herring oil, behave similarly to cod liver oil during blowing (Fig. 2), and various amounts could be blended with the cod liver oil before or after blowing. As shown in Fig. 2, the decrease in iodine value when blowing seal oil or herring oil parallels the decrease in cod liver oil, while the increase in viscosity is almost the same in the three oils.

VISCOSITY

The increase in viscosity varies with the temperature and the airflow. In Fig. 1 the viscosity is plotted against time at several temperatures and at constant air flow. It can be seen that to blow cod liver oil to a high viscosity, e.g. higher

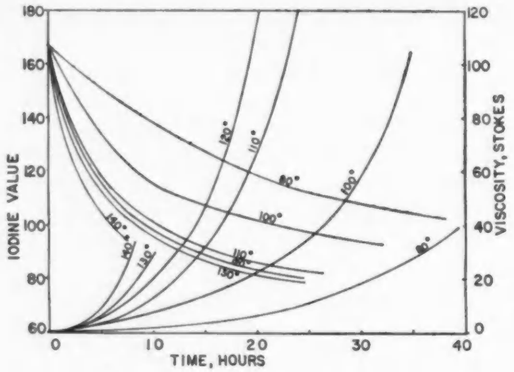

FIG. 1. Effect of temperature (°C) of blowing on iodine value and viscosity. Curves reading upward to the right indicate changes in viscosity; downward to the right, changes in iodine value. Air flow constant at 6,500 ml/min.

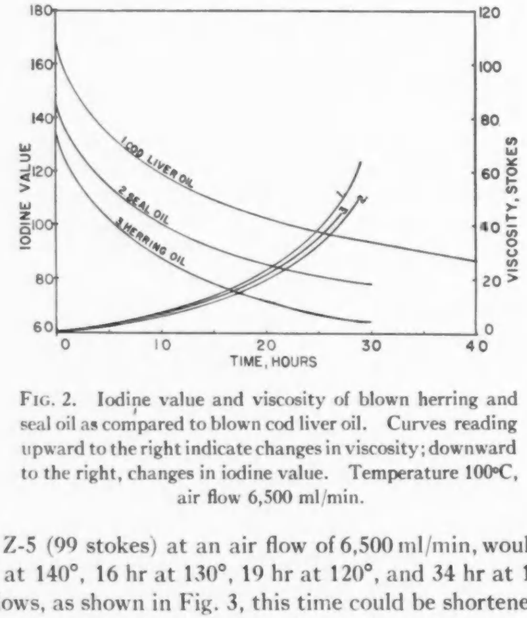

FIG. 2. Iodine value and viscosity of blown herring and seal oil as compared to blown cod liver oil. Curves reading upward to the right indicate changes in viscosity; downward to the right, changes in iodine value. Temperature 100°C, air flow 6,500 ml/min.

than Gardner Z-5 (99 stokes) at an air flow of 6,500 ml/min, would take approximately 11 hr at 140°, 16 hr at 130°, 19 hr at 120°, and 34 hr at 100°. However, at higher air flows, as shown in Fig. 3, this time could be shortened considerably. Since approximately 10,000 ml/min was the maximum the sintered glass plate could handle, a levelling off in the rate of viscosity increase with increased air flow was not reached.

By plotting oil viscosity vs. time on semi-log paper, a nearly linear relationship was found (Fig. 4). The points not falling on a straight line were in most cases samples taken when the temperature had fluctuated from the average. Gillam (1949) also plotted his results obtained by blowing rapeseed oil on a logarithmic scale and found a linear relation after the induction period and up to the point when gelation occurred.

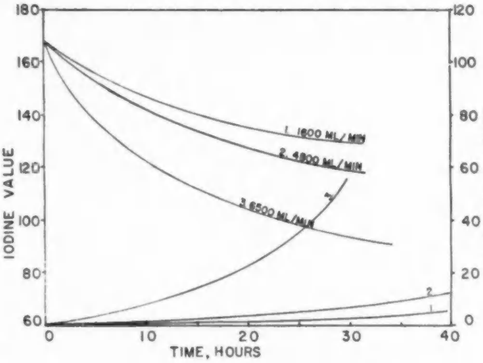

FIG. 3. Effect of air flow on viscosity and iodine value. Curves reading upward to the right indicate changes in viscosity; downward to the right, changes in iodine value. Temperature constant at 100°C.

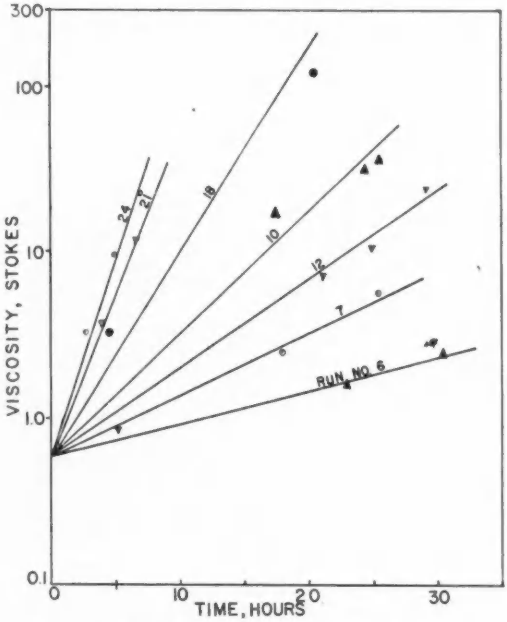

FIG. 4. Logarithmic relation between viscosity and blowing time.

Free Fatty Acids (FFA)

When blown oils are to be used for lubricating purposes, a FFA content higher than 3% is considered undesirable. In Fig. 5, the development of FFA during blowing of cod liver oil is plotted. In most runs the FFA did not rise above 4.5 to 5%. Most of these acids are formed as a result of peroxide decomposition to give chain scission, so alkali refining of the starting material only lowers the final FFA content by the same number of units as the original difference in FFA content of the two oils. The formation of acids seems to proceed at the same rate in the alkali-refined oil as in the untreated oil. Bukowiecki (1958) in a study of corrosion in connection with fatty oils in lubrication, pointed out that attack on iron is not related to the total acidity of the oil but rather to the volatility and reactivity of the acids formed.

At higher temperatures (130 to 140°) the increase in viscosity is relatively much more rapid than the increase in FFA since some lower-molecular-weight acids would blow off at these temperatures. This suggests a method for lowering the FFA content closer to 3% by raising the temperature and increasing the air flow toward the end of the processing; however, this is apt to darken the oil excessively. Steam distillation was tried as an alternative method, with good results. In a 7-hr run at 130° with an air flow of 9,500 ml/min, the FFA content was 3.6%. By blowing steam through for 20 min, the FFA dropped to 3.1% with no effect on the colour. According to Gillam (1949), some esterification of the acids with hydroxyl groups will occur. However, in one run (No. 22) glycerol was added to possibly esterify some of the FFA, but the temperature (130°) was too low for uncatalyzed esterification (Markley, 1961, p. 798), and no reduction in FFA was observed.

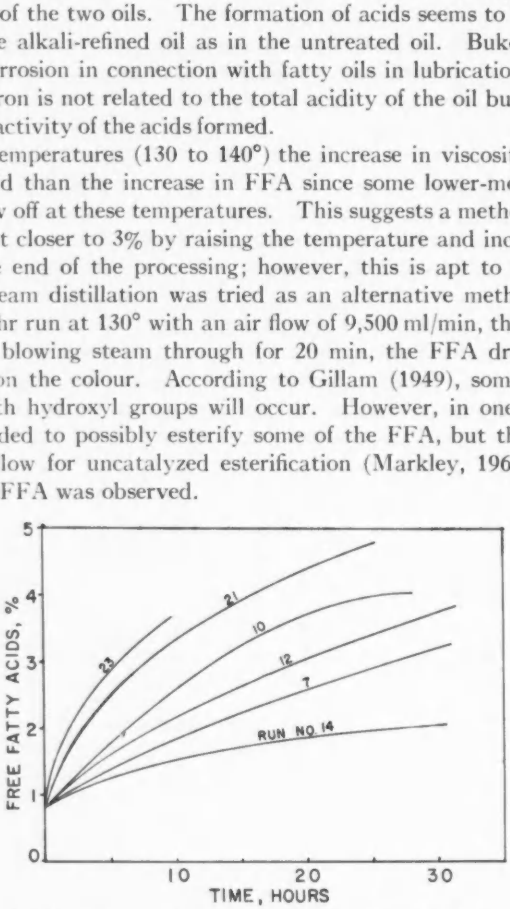

Fig. 5. Effect of blowing time on formation of free fatty acids.

Catalysts

A few experiments were also carried out using catalysts, e.g. boron trifluoride, and calcium and cobalt driers. The cobalt drier (0.013% cobalt to oil) was found to be most effective in promoting polymerization, as shown in Fig. 6. However, the iodine value dropped only to 99 which is considered too high for blown oils to be used in lubrication. Also, the polymerization continued on storage, a tough film forming on the surface. The use of 0.025% boron trifluoride also accelerated the polymerization, but 0.0042% calcium produced a product only slightly better than the untreated oil. The use of these catalysts would therefore not be considered advantageous in view of the high iodine value. The catalysts would have to be neutralized or removed, adding to the cost of the blown oil (Eichwald, 1939; Whiteley and Turner, 1941).

REFRACTIVE INDEX

The refractive index increased with blowing time as shown in Fig. 7, and represents the easiest and quickest analytical method to check on the progress of the blowing once calibration has been achieved.

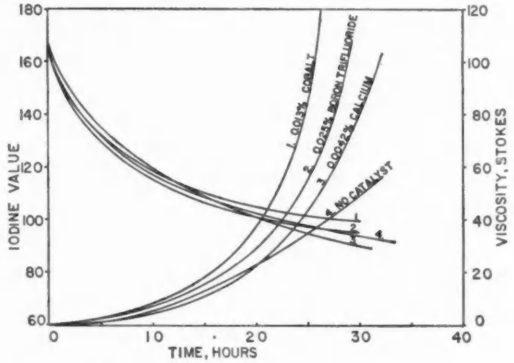

FIG. 6. Effect of catalysts on viscosity and iodine value. Curves reading upward to the right indicate changes in viscosity; downward to the right, changes in iodine value. Temperature 100°C, air flow 6,500 ml/min.

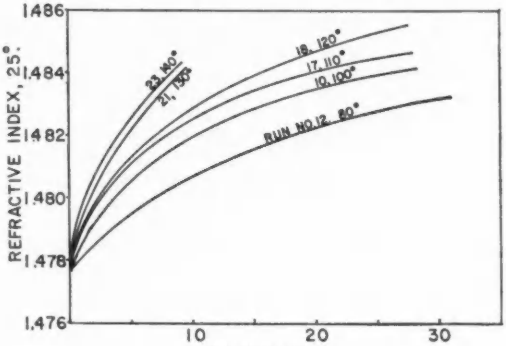

FIG. 7. Effect of blowing time on refractive index.

Colour

The colour was not objectionably dark in most of the samples, the darkest products being from the runs at higher temperatures and using certain catalysts. By using high air flows to shorten the blowing time as much as possible, products with a Gardner colour of 11 to 12 should be attainable.

Settling

The only samples that showed any appreciable settling out from a 10% solution in LCT 20 after 1 month at room temperature, were samples from runs No. 9, 14 and 15. These runs were catalyzed by driers or boron trifluoride, indicating that these oils cannot be used in lubrication without further treatment. Settling tests at other concentrations or temperatures were not attempted.

An attempt was made to correlate the settling out with hydroxyl content of the blown oils and also by comparison of the near-infrared spectra. It was found that the hydroxyl values of a blown oil showing settling out (No. 14), and oils blown at 100 and 120° (No. 10 and 18) were nearly the same (1.2 to 1.5% OH). The near-infrared spectra of the three samples were also nearly identical, all showing a broad maximum at 2860 mμ.

SUMMARY

There is no doubt that a blown oil for lubrication purposes could be prepared from cod liver oil or certain other marine oils. Some preliminary experiments would have to be carried out with the plant as the type of vessel, blower, etc. would seriously affect the product. The blown oil would probably have to be steam treated to remove odour and to lower the FFA content.

The present study correlates temperature, time and air flow with iodine value, viscosity and FFA as a guide to large-scale air blowing operations with certain marine oils.

Samples from the products of the present study have not been evaluated under the conditions laid down by the oil companies since some minor adjustments in specifications may be required, particularly in iodine values and FFA. These adjustments may, however, be possible due to the price advantage of marine oils vis-à-vis vegetable oils.

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Seasonal Changes in Feeding of Coho and Chinook (Spring) Salmon in Southern British Columbia Waters[1]

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ABSTRACT

Food study based on the stomach analyses of 551 chinook salmon (*Oncorhynchus tshawytscha*) and 659 coho salmon (*O. kisutch*) collected from the various localities along the southern British Columbia coast during the summer of 1957 revealed that herring followed by crustaceans formed the most important items of the diet of the two species. Coho salmon exhibited a more pelagic and varied diet than chinook salmon caught in the same area. Definite seasonal fluctuations in the composition of food and feeding intensity were noticed. Considerable amounts of Crustacea were taken in early summer months and after that fish assumed importance.

Qualitative and quantitative differences in the feeding of these two species on the east and west coasts of Vancouver Island appear to warrant the establishment of two food type areas. Although herring constitute the major food item of both spring and coho salmon, evidences are presented in support of the hypothesis that a change in herring stock is not likely to affect salmon abundance in British Columbia coastal waters.

INTRODUCTION

Due to rapid growth of the trolling fleet in British Columbia coastal waters in recent years and increasing exploitation of coho and spring salmon stocks, much concern has been aroused among the commercial and sport fishermen about the conservation of these species of Pacific salmon. As spring and coho salmon stocks are fished extensively in coastal waters of southern British Columbia prior to their entering the freshwater streams, a closer appraisal of the catch composition, life history of the fish and adequacy of existing regulations for the purpose of conservation has become an important part of the general investigation program of the Fisheries Research Board of Canada. The present study deals with seasonal changes in food and feeding of coho and spring salmon during their coastward migration.

MATERIAL AND METHODS

Samples for food study were obtained mainly from those areas around Vancouver Island where the commercial fishing is most active and sampling could be done with sufficient reliability. All the samples from the east and west coast of Vancouver Island were obtained from commercial and sport trollers, while those from the Fraser River and the Strait of Juan de Fuca areas were

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chiefly gill-net and purse-seine caught fish. In order to ensure uniformity in sampling, each collector was issued definite instructions (see Appendix), modified from those originally issued by Pritchard and Tester (1944).

Fishing areas around Vancouver Island included Barkley Sound, Clayoquot Sound, Nootka Sound, Kyuquot Sound and Cape Cook on the west coast and Nanaimo, Courtenay and the southern portion of the Strait of Georgia on the east coast (Fig. 1).

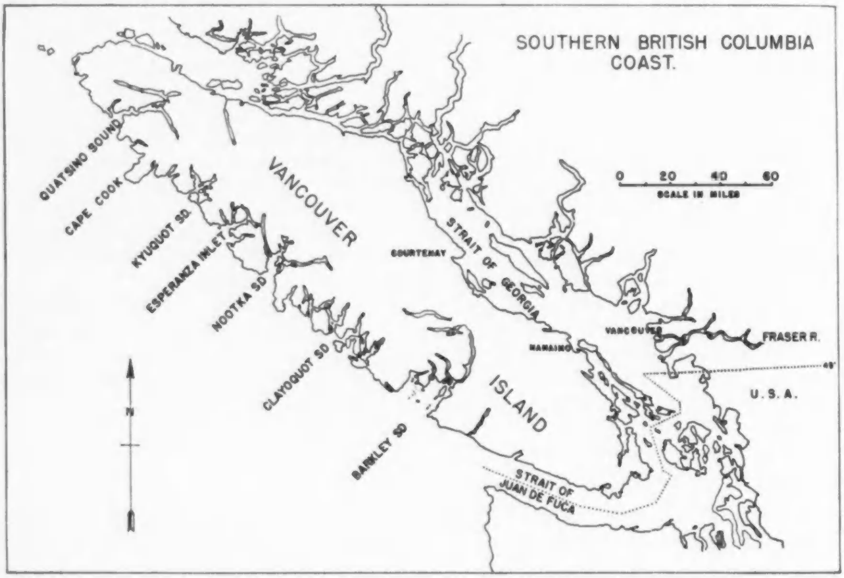
SOUTHERN BRITISH COLUMBIA COAST.
0 20 40 60
SCALE IN MILES
QUATSINO SOUND
CAPE COOK
KYUQUOT SD.
ESPERANZA INLET
NOOTKA SD
CLAYOQUOT SD
BARKLEY SD
VANCOUVER
ISLAND
COURTENAY
STRAIT OF GEORGIA
NANAIMO
VANCOUVER
FRASER R.
49°
U. S. A.
STRAIT OF JUAN DE FUCA
N

FIG. 1. Map of southern British Columbia coast showing location of sampling areas.

Stomachs were examined from 659 coho and 551 spring salmon collected during May-October, 1957, of the sizes shown in Tables I and II. Food items were sorted to the most specific category to which they could be identified. In those stomachs where the food items were found in an advanced state of digestion, identification of fish was possible only to the generic level by means of opercle bones, vertebral column, otolith, appendages, etc. The quantitative analysis was done by the volumetric method, in which the volume of each item of food is expressed as a percentage of the volume of the total stomach contents (Hynes, 1950). The prevalence of each item of food in the diet during different months was calculated by the occurrence method in which the number of fish in which each food item occurs is expressed as a percentage of the total number of fish examined. From individual data monthly averages were calculated and from these the total percentage composition by volume and occurrence was determined.

Troll-caught samples are dealt with separately from those caught by gill net or purse seine for the following reasons: (1) Trolling with lures is no doubt selective to feeding fish. (2) Fish caught by methods other than trolling are not cleaned or dressed soon after their capture, and post-mortem digestion and deterioration of stomach contents occurs. (3) Fish caught in seines or gill nets are subject to excessive handling and have been seen to disgorge their stomach contents more often than troll-caught fish. (4) Netting in the Strait of Juan de Fuca and the Fraser River commenced late in the season, and samples could be procured only after July (for spring) and August (for coho) when many of the fish had stopped feeding as they approached maturity.

TABLE I. Number and size of coho salmon collected each month from various areas in 1957. V.I. = Vancouver Island.

Month	Area	Fish examined	Fork length	
			Mean	Range
		no.	*cm*	*cm*
May	E coast of V.I.	18	47	43–53
	W coast of V.I.	2	52	51–53
June	E coast of V.I.	48	53	46–59
	W coast of V.I.	16	58	55–64
July	E coast of V.I.	57	52	40–58
	W coast of V.I.	41	62	54–73
August	E coast of V.I.	13	52	25–66
	W coast of V.I.	85	64	51–74
	Juan de Fuca	129	59	40–71
September	E coast of V.I.	5	49	46–52
	W coast of V.I.	45	66	56–72
	Juan de Fuca	87	65	45–77
	Fraser River	32	68	54–80
October	Fraser River	81	61	53–80
Total		659		

TABLE II. Number and size of spring salmon collected each month from various areas in 1957. V.I. = Vancouver Island.

Month	Area	Fish examined	Fork length	
			Mean	Range
		no.	*cm*	*cm*
May	E coast of V.I.	9	63	56– 79
	W coast of V.I.	35	64	11– 90
June	E coast of V.I.	16	64	38– 79
	W coast of V.I.	53	71	13–103
July	E coast of V.I.	29	54	23– 96
	W coast of V.I.	57	76	56–108
	Fraser River	64	66	27– 95
August	E coast of V.I.	6	59	30– 79
	W coast of V.I.	67	71	33– 96
	Juan de Fuca	36	66	48– 90
	Fraser River	60	67	46– 90
September	E coast of V.I.	5	26	24– 27
	W coast of V.I.	32	76	60– 96
	Juan de Fuca	34	81	46–106
	Fraser River	35	78	55–104
October	Fraser River	13	83	55– 99
Total		551		

COHO SALMON (*ONCORHYNCHUS KISUTCH*)

Diet and Seasonal Composition

Stomach contents have been classified into three main categories: (1) fish, (2) Crustacea, and (3) miscellaneous (gastropods, jellyfish, plant matter, detritus, digested matter, slime, etc.). Stomach content analyses for troll-caught coho are summarized by months and areas in Table III and Fig. 2. The relative importance of the various food items in the diet is shown in Fig. 4.

Fish, chiefly herring and sand lance, and crustaceans (euphausiids, amphipods and megalops larvae) were the most important food items. Pacific herring (*Clupea harengus pallasi*) constituted 72% of the total volume and were present in 21% of the specimens examined. The largest volumes per fish were found in July in the Strait of Georgia and in August off the west coast of Vancouver Island. Although various sizes of herring were found, fish measuring 14 to 23 cm in fork length were most common in the stomachs. This size range includes a great majority of herring which are of Age III or younger and have not yet been recruited to the herring fishery. Herring approaching 3 and 4 years of age make up 80 to 90% of the commercial catch, which takes place in the autumn and early winter (Taylor, 1955). Juvenile herring of the first year, 2.5 to 9.0 cm in fork length, were found most commonly in the stomachs of specimens collected from the Nanaimo area in the Strait of Georgia in May and June. The average size of herring eaten by west coast coho was larger than those taken by east coast coho.

Sand lance (*Ammodytes hexapterus*) contributed 5% of the total volume of food and occurred in 6% of the stomachs. Other fishes included occasional specimens of rockfish (*Sebastodes* spp.), Pacific saury (*Cololabis saira*), threespine stickleback (*Gasterosteus aculeatus*), unidentifiable clupeids and other fish remains.

Euphausiids appeared as the most important item in the crustacean diet of coho making up 9% of the total volume and occurring in 13% of the stomachs. They were found in almost all areas of the east and west coasts but were most abundant in the Strait of Georgia during June and September. Two types of euphausiids were distinguished and identified by the author—a red variety, *Thysanoessa spinifera* and a white variety, *Euphausia pacifica*.

Amphipods also contributed significantly to the crustacean diet and like euphausiids were most abundant on the east coast of Vancouver Island. Both hyperiid and gammarid amphipods occurred, the latter more frequently. Young crabs and crab megalops, like other crustaceans, had seasonal fluctuations. Different types and sizes of megalops larvae were present but only those belonging to *Cancer magister* were identified. Occasional shrimps and copepods comprised the other Crustacea; none of these formed a significant portion of the diet of coho salmon at any time.

During early summer months, crustaceans constituted a significant portion of the diet of cohoes but after June they were replaced largely by a fish diet, chiefly Pacific herring, which reached its peak in August on the west coast forming 84% of the volume of food. In September fish formed 75% of the food but euphausiids and megalops equalled the fish in incidence. Sand lance remained relatively unimportant and more or less uniform in the diet for the entire period.

TABLE III. Percentage composition (A) and frequency of occurrence (B) of diet constituents in the stomachs of troll-caught coho salmon from east and west coasts of Vancouver Island in 1957; column C shows the number of stomachs in which each item occurred.

	May			June			July			August			September		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
EAST COAST															
Herring	50.9	44.4	8	20.1	14.6	7	58.2	35.0	20	8.8	7.7	1	...	...	...
Sand lance	...	...	...	1.5	8.3	4	0.6	5.3	3	6.3	7.7	1	...	...	...
Other fishes	7.1	22.2	4	5.2	45.8	22	13.0	38.6	22	6.3	23.1	3	12.5	20.0	1
Euphausiids	13.8	22.2	4	27.8	33.3	16	0.1	3.5	2	18.8	7.7	1	43.7	40.0	2
Amphipods	24.3	88.9	16	29.8	66.7	32	19.2	28.0	16	43.9	61.5	8	...	...	...
Megalops	3.9	27.8	5	15.1	52.1	25	8.2	21.0	12	15.0	15.4	2	25.0	20.0	1
Other crustaceans	...	5.5	1	0.2	10.4	5	0.1	7.0	4	0.9	15.4	2	18.8	20.0	1
Miscellaneous	...	...	...	0.3	12.5	6	0.6	2.0	1	...	...	...	...	...	...
Total vol. (*cc*)		68.2			430.8			328.7			79.7			8.0	
No. examined		18			48			57			13			5	
WEST COAST															
Herring	...	...	...	65.4	18.7	3	74.4	36.6	15	87.2	44.7	38	69.7	35.5	16
Sand lance	...	...	...	1.3	12.5	2	3.5	9.7	4	7.6	14.1	12	4.6	6.7	3
Other fishes	...	...	...	3.0	37.5	6	8.1	46.3	19	1.0	10.6	9	0.9	8.9	4
Euphausiids	...	...	...	5.6	31.2	5	0.8	9.7	4	3.4	23.5	20	22.1	28.9	13
Amphipods	...	...	...	0.2	25.0	4	0.1	7.3	3	...	...	...	...	...	...
Megalops	...	...	...	24.5	75.0	12	12.7	46.3	19	0.5	9.4	8	2.3	17.8	8
Other crustaceans	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Miscellaneous	...	...	...	...	...	...	0.4	7.3	3	0.5	8.2	7	0.4	6.7	3
Total vol. (*cc*)					185.0			709.5			2,172.5			583.0	
No. examined		2			16			41			85			45	

Food Type Areas

Milne (1950) reported that coho salmon taken in the Strait of Georgia are smaller than those caught off the west coast of Vancouver Island. These small coho are popularly known as "bluebacks" and are fished mostly from June to September, with peak catches in June and July. Special emphasis was placed on the collection of simultaneous samples from the Strait of Georgia and the west coast of Vancouver Island. In the Strait of Georgia Crustacea exceeded fish in volume except during May and July (Fig. 2). Amphipods were the most important crustaceans for inside coho, while euphausiids and crab megalops were next in order.

Off the west coast, by contrast, fish were never less than 70% of the coho food. It seems possible that the slower growth of the Strait of Georgia coho as compared with outside cohoes is related to the differences in their food and feeding conditions. The above is supported by the data collected by Milne and others during 1950, 1953, 1954, and 1956 and summarized by Prakash and Milne (1958).

Feeding Intensity

To show the fluctuations in feeding intensity of coho salmon, average volume of food per stomach was calculated for each month from May to September. This average included fish with empty stomachs. To correct approximately for change in size of fish, volumes were also expressed as "volume of food per 10 centimetres of fish length". As this index is liable to be influenced by the type of food organisms in the diet, particularly large volumes of fish, and may not give a true picture, another feeding index was used, viz., percentage of stomachs containing food (Fig. 3).

More fish caught in the Strait of Georgia were feeding, and they ate more, during May and June than thereafter. West coast coho also exhibited a similar trend in proportion that were feeding (Fig. 3) but the average volume of food per stomach steadily increased from May to August, with a sudden drop in September (Fig. 2). Feeding intensity for samples from the Strait of Juan de Fuca in August and September and the Fraser River in September and October showed considerable decline in both numbers and volume.

About 95% of troll-caught coho from the east and west coasts of Vancouver Island belong to age group 3_2 (Gilbert system) and are in the last year of life on their spawning migration (Pritchard, 1940). Figure 3 shows that there is a marked decrease after August in the rate of feeding as the fish populations are maturing and move from the west coast of Vancouver Island towards freshwater streams, intermediate conditions of feeding being represented in the Strait of Juan de Fuca, with fish caught in the Fraser River exhibiting very little feeding.

CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*)

Diet and Seasonal Composition

The results of analyses of the stomach contents during various months are presented in Table IV. The relative importance of fish and Crustacea in the diet of spring salmon from the east and west coasts of Vancouver Island is shown in Fig. 2.

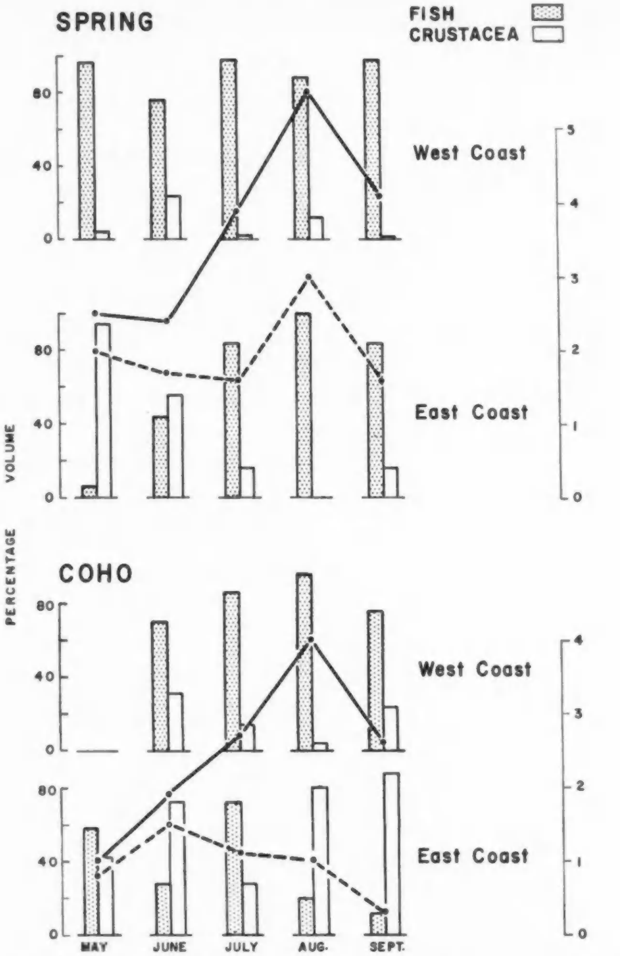

FIG. 2. Monthly variations in feeding intensity and the volume of fish and Crustacea eaten by coho and spring salmon on the east and west coasts of Vancouver Island, 1957. *Bars*: percentage volume (left-hand scale); *Lines*: average volume of food per 10 cm of fish length (right-hand scale).

The food of spring salmon is similar to that of coho, though somewhat less varied (Fig. 4). Spring salmon subsisted largely on herring which constituted 72.5% of the total volume of food. Percentage occurrence of herring in the stomachs examined was much greater than that found in coho. The size of herring eaten by spring salmon ranged from 3.5 to 24 cm in fork length but the size range most commonly taken was 13 to 23 cm for the west coast springs and 5 to 10 cm for the Strait of Georgia springs. Large springs usually contained a higher percentage of herring and consumed larger herring than did small springs. No trace of pilchards was found in any of the stomachs examined; earlier investigations, done when pilchards were quite common off the British Columbia coast, had reported them as an important item (Chapman, 1936; Pritchard and Tester, 1944).

Sand lance follow herring as the next most important food item, and contribute 13.6% of the total volume of food. They range from 6 to 21 cm in fork length, though uniform-sized fish were usually found in individual stomachs. There was no suggestion that abundance of sand lance was associated with particular areas; Pritchard and Tester (1944) reported an abundance of sand lance along the northwestern coast of Vancouver Island. Other miscellaneous fish included Pacific saury, rockfish, Pacific cod (*Gadus macrocephalus*), sand fish (*Trichodon trichodon*) and a few unidentified clupeids.

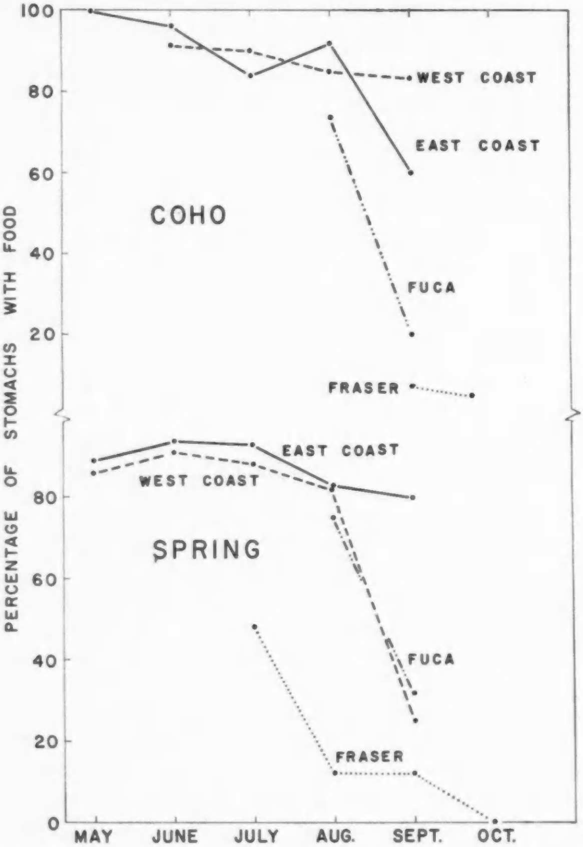

FIG. 3. Percentage of spring and coho salmon stomachs with food, by month and by area.

TABLE IV. Percentage composition (A) and frequency of occurrence (B) of diet constituents in the stomachs of troll-caught spring salmon from east and west coasts of Vancouver Island in 1957; column C shows the number of stomachs in which each item occurred.

	May			June			July			August			September		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
EAST COAST															
Herring	4.3	11.1	1	28.9	37.5	6	73.7	41.4	12	25.7	33.3	2	85.0	40.0	2
Sand lance	1.7	11.1	1	0.6	6.2	1	1.3	6.9	2	13.8	16.7	1	...	...	...
Other fishes	...	...	...	15.0	43.7	7	8.1	34.5	10	60.5	50.0	3	...	...	...
Euphausiids	94.0	77.8	7	53.8	37.5	6	16.3	10.3	3	...	...	...	...	...	...
Amphipods	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Megalops	...	...	...	...	...	...	0.2	3.4	1	...	...	...	2.5	20.0	1
Other crustaceans	...	11.1	1	1.7	12.5	2	0.1	6.9	2	...	...	...	12.5	40.0	2
Miscellaneous	...	...	...	...	...	...	0.3	10.3	3	...	...	...	...	...	...
Total vol. (*cc*)		116.6			176.5			260.1			209.0			20.0	
No. examined		9			16			29			6			5	
WEST COAST															
Herring	25.5	8.6	3	49.5	35.8	19	83.0	38.5	22	73.8	41.8	28	98.6	50.0	16
Sand lance	68.4	31.4	11	21.6	22.6	12	13.9	26.3	15	19.1	19.4	13	...	...	...
Other fishes	1.4	14.3	5	4.3	26.4	14	0.6	8.8	5	0.5	4.5	3	0.9	9.4	3
Euphausiids	2.7	25.7	9	19.2	11.3	6	2.2	12.3	7	4.7	6.0	4	0.2	3.1	1
Amphipods	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Megalops	1.0	5.7	2	4.8	26.4	14	0.1	3.5	2	...	...	...	...	...	...
Other crustaceans	0.2	8.6	3	0.6	7.5	4	0.1	3.5	2	0.8	6.0	4	...	...	...
Miscellaneous	0.8	14.3	5	...	...	...	0.1	7.0	4	1.1	11.9	8	0.3	9.4	3
Total vol. (*cc*)		563.8			888.4			1,679.3			1,946.5			1,160.6	
No. examined		35			53			57			67			32	

The crustacean diet was composed of euphausiids, young crabs, crab megalops and other miscellaneous forms of minor importance. Euphausiids were the dominant items in crustacean diet making up 10% of the total volume of food. No amphipods were found in any of the stomachs examined throughout the period May to September.

Table IV shows changes in occurrence of the various food components in the stomachs of spring salmon during the 5-month period. Sand lance predominated only in May, especially in samples from Barkley Sound. After May, herring assumed importance and the largest volumes of herring per fish were found in July in the Strait of Georgia and in August and September off the west coast. Considerable quantities of euphausiids were taken in May and June but declined afterwards. Crab megalops and other crustaceans did not contribute much to the diet and no appreciable seasonal trends were noticeable.

FOOD TYPE AREAS

In spring salmon, quantitative differences in the food on the two coasts were evident but, except for an abundance of crustaceans taken during May and June on the east coast, there was little to suggest that the diet of spring salmon differed qualitatively as in the case of cohoes (Fig. 2). Samples obtained from the Fraser River gill-net fishery showed little food in general. The only food found in these samples was sand lance; no herring were noticed. Strait of Juan de Fuca springs were found feeding largely on herring and Crustacea (mainly euphausiids), with no trace of sand lance. As in coho salmon, the average size of spring salmon is smaller in the Gulf of Georgia than off the west coast (Table II). A few samples taken from the Gulf of Georgia in September were exceptionally small and were feeding heavily on juvenile herring.

FEEDING INTENSITY

Feeding intensity of 551 spring salmon as calculated on the basis of average volume of food per stomach and per 10 cm of fish length (Fig. 2) and also on the basis of percentage of stomachs containing food (Fig. 3) revealed definite fluctuations for the period May to October.

Larger quantities of food were found in fish from off the west coast of Vancouver Island than in those from off the east coast but more fish had food in their stomachs in the latter area. Spring salmon from the Strait of Georgia showed a slight downward trend in the amount of food from May to July, after which feeding increased probably due to the abundance of young herring in the Strait of Georgia. Total volume of food was highest both for the east and west coast fish in August (Fig. 2) but more fish were feeding in June (Fig. 3). Considerable decline in feeding occurred after August on both coasts as revealed by food indices and percentage of stomachs containing food (Fig. 2, 3). Samples of mature fish obtained from the mouth of the Fraser River from July to October showed little food and a declining feeding trend which became most pronounced in October. Samples from the Strait of Juan de Fuca showed feeding conditions intermediate between those found in the west coast and Fraser River fish. This situation is very similar to that seen for Fuca coho in the earlier section.

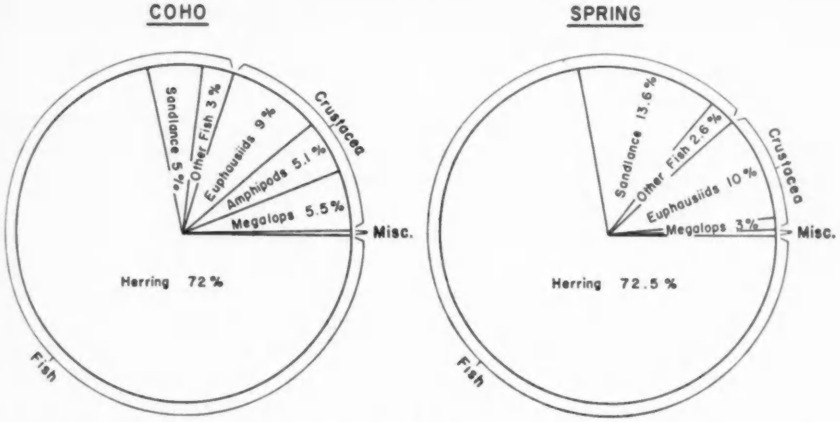

FIG. 4. **The relative importance of the various food components in the diet** of troll-caught coho and spring salmon sampled in 1957 in southern British Columbia coastal waters.

DISCUSSION

The data presented in this paper, as well as the findings of earlier investigators, indicate that although spring and coho salmon are essentially piscivorous when adult, they do exhibit considerable plasticity in their feeding habits and their fish diet is not confined to any one species. Williamson (1930) studied the food of spring salmon off the west coast of Vancouver Island and found that sand lance formed the principal food, whereas, pilchard, herring, euphausiids and megalops made up the rest of the diet. Chapman (1936) found pilchard as the most important single item in the diet of spring salmon caught off the Washington coast. Pritchard and Tester (1944), in their study of food of spring and coho salmon off British Columbia coast, found that herring constituted the most important food item off Barkley Sound and sand lance off Quatsino Sound. Merkel (1957) reported that northern anchovy and rockfish formed the major food of chinook salmon in the vicinity of San Francisco.

From these studies it is evident that the food of salmon changes with locality and time (season). Changes in the diet of spring and coho salmon are probably more a function of changes in availability of a particular food item than of possible selection on the part of the fish. Silliman (1941) reported two distinct phases of feeding for chinook and coho salmon taken off Washington—an invertebrate feeding phase and a fish feeding phase. His data indicated that fish collected from the region of Westport and Neah Bay subsisted largely on crustaceans during May and June and on fish after that. Similar seasonal changes have been reported by Merkel (1957) for chinook salmon in the vicinity of San Francisco.

Evidence in support of food differences according to locality comes from the studies conducted on the food of coho salmon in 1956 as a part of the International North Pacific Fisheries Commission's program of investigations. Preliminary observations revealed that squids form an important item of coho diet in the high seas (personal communication from Dr F. Neave and Mr J. I. Manzer). All fish samples having squids in their stomachs were taken far out in the Pacific Ocean, while those caught close to the coast contained euphausiids. Qualitative differences in food according to area have also been reported by Chapman (1936) for coho salmon off the Washington coast. He found that at Neah Bay near the entrance to the Strait of Juan de Fuca the coho subsisted chiefly on Crustacea, whereas off the coast at Westport fish formed the dominant food item.

Both adult and juvenile herring have been shown as the most important item of diet of spring and coho salmon off the British Columbia coast in the present study, but available data also suggest that in the absence of herring, salmon would feed on alternative foods. In the light of what has been stated above, it is questionable that a possible change in herring stocks would influence salmon abundance as most fishermen believe. While a decline in the abundance of herring can be expected to be compensated by a greater dependence on other food organisms, the number of salmon is unlikely to be affected by the scarcity of any one kind of food unless the availability of alternative foods is also markedly reduced.

The chief difference between the diet of spring and coho salmon is the larger variety of food items taken by coho. Similar trends have been reported by Pritchard and Tester (1944), Kirkness (1948), Heg and Van Hyning (1951) and Reid (1961). While large spring salmon consume more herring than small springs, such a relationship is not established for coho salmon. The latter, particularly those caught on the east coast of Vancouver Island, ate substantial quantities of crustaceans in addition to fish. Based on the data in hand, it seems reasonable to attribute some of this difference to the depth which these two species of Pacific salmon inhabit. Spring salmon are known to migrate at greater depths and closer to shore than coho salmon. Most are taken by commercial trollers along the continental shelf below 10 fathoms (18 m). Most coho salmon, on the other hand, are caught in the top 10 fathoms and farther from the shore, thereby exhibiting a more pelagic existence (Milne, 1957).

It has been suggested that the consumption of the food components by the salmon at various stages of their migration is subject to considerable variation, probably being associated with the abundance of the food organisms and the extent of their availability (Andrievskaya, 1957). Food indices on the west coast of Vancouver Island show intense feeding activity especially in the month of August and a considerable drop thereafter. There is a marked decrease in the rate of feeding as the fish move from the east and west coasts towards freshwater streams. A significant increase in the number of empty stomachs is also noticeable as the season advances and the area of sampling shifts towards freshwater streams. It appears that this decline in feeding intensity is more a function of some physiological activities associated with gonad maturity than that of nonavailability of specific food items because of marked differences in the extent of feeding of fish having the gonads in different stages of maturity (Prakash, 1958).

It has already been suggested that the east and west coasts of Vancouver Island represent two feeding areas which are probably different so far as the amount of food available during summer months is concerned. The west coast is characterized by lower and more uniform temperature and high salinity (Pickard and McLeod, 1953). The east coast on the other hand presents quite opposite conditions, viz., high summer temperature and low salinity mainly due to Fraser River run-off of fresh water (Waldichuk, 1957). The differences in the productivity on the two coasts seem largely to be influenced by different oceanographic conditions. Northwest winds in the summer off the west coast of Vancouver Island result in upwelling nutrient-rich water which could be expected to cause higher productivity. On the east coast, on the other hand, relatively high freshwater inflow during the summer months results in marked vertical stratification in the water which inhibits replenishment of nutrients in the upper layers and may thus reduce the general productivity (Tully and Dodimead, 1957). These differences in the productivity levels on the two coasts of Vancouver Island are reflected in part in the summer growth of spring and coho salmon sampled from these areas. Spring and coho salmon off the east coast of Vancouver Island are usually smaller than their counterparts on the west coast. This situation might be either due to lack of food in the Strait of Georgia compared to the west coast or due to the presence of two differently growing stocks on the two coasts. Additional data are required to fully assess the variations in growth pattern.

SUMMARY

1. Analysis of stomach contents of spring and coho salmon taken from southern British Columbia coastal waters revealed that Pacific herring and crustaceans formed the most important items of their diet during the summer of 1957.
2. While the main items of diet of spring and coho salmon are essentially similar, the latter appear to accept a wider variety of food items than the former. This difference is probably associated with the depth which these two species inhabit, the coho being more pelagic in its feeding migration.
3. Definite seasonal changes in the composition of food of coho and spring salmon were observed. During May and June, Crustacea formed the dominant food but later fish replaced Crustacea. Both in quantity eaten and prevalence in the stomachs, amphipods appeared to be of outstanding importance in the diet of coho salmon, whereas no amphipods were found in any spring salmon stomachs.
4. Both spring and coho salmon, particularly those from the west coast of Vancouver Island, show intense feeding activity during July and August. After August, feeding intensity takes a declining trend which appears to be associated with gonad maturity of the migrating stock.
5. The east and west coasts of Vancouver Island represent two food type areas with respect to the amount of food available to coho and spring salmon and the type of food items consumed.

6. Available data suggest that although Pacific herring is the most important single item of spring and coho diet, these fish would feed on alternative food items if there were no herring available. Hence, it is unlikely that the abundance of salmon would be affected if there was a change in herring stock abundance.

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APPENDIX

INSTRUCTIONS FOR THE COLLECTION OF STOMACHS AND GONADS OF SPRING AND COHO SALMON

Each collector is being provided with kits made up of one liver can, one quart of formalin, and 25 numbered bags. Upon receipt of this shipment, the bags should be removed and kept separately, the formalin emptied into the liver can and the can filled to approximately one half its capacity with salt or fresh water.

In order to have a representative sample, it is suggested that they should be spread throughout the period of fishing by taking either 5 or 10 samples a week. Fishermen are asked to collect stomachs and gonads in an unbiased and random way.

In large fish remove the U-shaped stomach by severing the gullet immediately behind the mouth and the intestine immediately behind the finger-like sacs (pyloric caeca) also remove each reproductive organ (gonad) making certain that each stomach and gonad is complete. In small fish remove entire gut and complete contents of body cavity and place them in the bag, tighten the drawstring and tie it around the top of the bag. In the book provided record the label number, date of capture, the fishing location, the fork length in centimetres and at least 5 scales from the left side of fish, and any other remarks.

Insert the bag and contents into the formalin solution in liver can.

The kit should be considered full when there is still enough formalin left to cover the bags. At this time close the lid tightly, and ship the package freight or express collect to the Biological Station, Nanaimo, B.C. Please mark on the return address so that further equipment and cheque to cover 25 cents payment on each sample may be delivered.

Your contribution is only part of a program throughout British Columbia. The analyses of these should serve as a basis for determining:

1. the actual food of the spring and coho salmon taken in the commercial catches;
2. the relative value of herring and shrimp in the food relationship;
3. the degree of maturity for different sizes of fish caught.

The investigators would welcome any data from log books or other records which have been collected in the past. Credit will be given for such data and they will be treated as strictly confidential.

PLEASE NOTE!

a) Separate marked cans should be used for spring and coho salmon.

b) Mail the envelope provided to Biological Station with information as to when each kit is dispatched.

c) If fish is undersized and small enough to go into the bag, make a small slit in the underside and include the whole fish as the sample.

Efficiency and Rate of Yolk Utilization by Developing Embryos and Larvae of the Pacific Sardine *Sardinops caerulea* (Girard)[1]

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ABSTRACT

The chemical composition of ripe Pacific sardine ovaries, composed primarily of yolk, is almost identical to that of yolk extracted from planktonic sardine embryos and larvae. Caloric measurements were made on ripe ovaries and the values obtained were used to estimate the caloric content of individual sardine embryos and larvae.

Water content of sardine egg and larval yolk averages 91.2%. An egg with a yolk volume of 0.56-mm^3 has a caloric reserve of 0.30 calorie when spawned. Caloric uptake from the embryonic and larval yolk was measured against time, and caloric utilization due to catabolic processes was analysed by indirect calorimetry (oxygen consumption) with changing embryological development and swimming activity. The caloric value of the remaining yolk 160 hours after spawning (at 14°C) is not sufficient to completely support the sardine larva's catabolic processes. This deficit is made up by resorption of tissue and is reflected in a loss of larval weight. Yolk is converted into tissue with an average assimilation coefficient of about 79%.

INTRODUCTION

Most pelagic fish larvae do not feed when hatched but have a yolk supply that provides their nutritional needs for growth and metabolism until feeding begins. Analyses of larval yolk afford an opportunity to study a food supply presumably ideally adapted to the metabolic requirements of the fish. Very little information has been available on the efficiency and rate that yolk can be utilized by embryos and larvae of pelagic fishes. This study presents such information for the pelagic embryo and yolk-sac larva of the Pacific sardine, *Sardinops caerulea* (Girard).

METHODS AND MATERIALS

The developing, pelagic egg of the Pacific sardine is approximately 1.7 mm in diameter (Ahlstrom, 1943) with a spherical yolk of about 1 mm in diameter enclosed in a subchorionic (perivitelline) space filled with sea water (Lasker and Theilacker, 1962a) and surrounded by a thin, turgid outer membrane, the chorion. An oil droplet, 0.2 mm in diameter, is oriented at the vegetal pole of the yolk sphere and the embryo initially develops at the opposite pole. At hatching, the sardine larva has not completed its embryological development and lacks a mouth, gills, and an open intestinal tract.

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Observations were made on ripe sardine ovaries to compare with those made on larvae. Maximum ovum diameters were measured for each ovary, and only those having eggs with diameters of 0.6 mm or greater and containing yolk uniformly distributed throughout, were considered ripe (MacGregor, 1957). Unlike other clupeids, e.g. the herring *Clupea harengus* (Blaxter, 1956), the female Pacific sardine is rarely taken in a running-ripe condition. This may be due to the short time interval, probably measured in hours, in which the already mature but opaque eggs imbibe or absorb water, become translucent, and are spawned.

The measurements described here were performed on fertilized sardine eggs and the larvae hatched from these eggs in laboratory jars. The developing eggs were taken in surface plankton hauls in the Pacific ocean off San Diego, California, at temperatures ranging from 14.2 to 17.0°C. The jars containing eggs were kept in a styrifoam insulated box until brought back to the laboratory where they were maintained at 14°C.

Respiratory measurements of individual sardine embryos and larvae were made with the reference diver technique described by Scholander *et al.* (1952). Results are given as oxygen consumed in microliters per single egg or larva per hour QO_2). The factors affecting the magnitude of respiration are discussed in an earlier paper (Lasker and Theilacker, 1962a). The method of extracting yolk from individual larvae was described earlier (Lasker and Theilacker, 1962a). Water content and percent dry weight were obtained by drying yolk at 75°C in pre-weighed capillary tubes to a constant weight. Weighings were made with an electrobalance to ±0.001 mg (Cahn Instrument Co., Paramount, California). Single larvae were weighed with this balance after rinsing them briefly in distilled water and by drying on small pre-weighed pieces of aluminum foil.

Embryonic and larval yolk volumes were calculated from photographs of eggs and larvae taken at intervals during the yolk consumption period. Intraovarian ovum diameters were measured by MacGregor's method (1957).

Total nitrogen (N) was determined by the standard micro-Kjeldahl procedure employing a Kirk still (Kirk, 1936) after sulfuric acid digestion with a selenized Hengar granule as a catalyst. Protein was calculated from the relationship N × 6.25 (Hawk *et al.*, 1954). Non-protein nitrogen of homogenized ovaries was determined after precipitation of protein with 10% trichloracetic acid and a Kjeldahl determination performed on the supernatant fluid.

Water in ovaries was determined by drying the tissue in a vacuum oven at 75°C to a constant weight. Other chemical measurements were made using the following techniques: carbohydrate (Somogyi, 1952); total lipid and phospholipid (Colowick and Kaplan, 1957; Bartlett, 1959). Ash was determined by combusting the dry ovary at 500°C and weighing the residue.

Caloric measurements were made with a bomb calorimeter utilizing a semimicro oxygen bomb (Parr Instrument Co., Moline, Illinois) after freeze-drying the tissue to be analyzed.

RESULTS

A knowledge of the degree of yolk dilution is necessary if accurate estimates are to be made of the organic material available to the larva from volume measurements of the yolk. Table 1 presents analyses of water content for 10 individual larval yolks. This shows there is little variation in water content from larva to larva. The water content of larval sardine yolk averages 91.2% as compared with the average of 70.7% found in ripe ovaries (Table I). I was fortunate in obtaining two running-ripe females whose eggs were exuding from the genital pore. Unlike the ova from the other ovaries examined, these ova were 1.2 mm in diameter, had translucent and swollen yolk, and the fat had separated into the discrete droplet characteristic of the planktonic egg. Both of these ovaries had over 88% water.

TABLE I. Analytical results. Mean values are followed by the standard deviation and (in brackets) the number of replicates. Yolk was obtained from spawned eggs. Ripe ovaries had maximum ovum diameters ranging from 0.6 to 1.0 mm.

	Larval yolk	Ripe ovaries
Percent water	91.2±1.4 (10)	70.7±1.5 (10)
Percent Total N, of dry weight	11.4 (2)	11.5±0.6 (10)
Percent protein, of dry weight (N × 6.25)	71.3	71.6
Percent fat, of dry weight	...	13.0±1.5 (11)
Calories per gram dry weight (bomb calorimeter)	...	5386±194 (9)

Protein is the chief yolk constituent in fishes (Smith, 1957), and amounts to over 70% of the yolk dry weight in the sardine. Because the yolk available from individual larvae was so small (<1 μl from each), analyses for caloric content had to be made on ripe ovaries; this was justified because their organic composition was almost identical. Analyses for total N showed that larval yolk and ripe ovaries have similar nitrogen content and that their protein electrophoretic patterns are indistinguishable, due to the fact that ripe ovary is composed almost wholly of ova containing yolk.

Phospholipids constituted approximately 11% of the dry weight of sardine eggs (range for 6 determinations, 8.2–12.5%). Glyceride fat was 4% of the total dry weight as calculated from the volume of the droplet and the specific gravity of sardine oil (Bailey, 1952). The qualitative and relative quantitative composition of the constituent fatty acids comprising the lipids found in spawned eggs was found to be identical to that of ripe ovary lipids (Lasker and Theilacker, 1962b). However, the variations in total fat recorded for ripe ovaries (Table I) may account for the slight differences found in caloric measurements between ovaries. The fat content of 16 ripe ovaries averaged 13.0%.

Tests for reducing substances before and after hydrolysis of sardine ovaries showed that there is less than 1% carbohydrate in dry ovarian tissue. Nonprotein nitrogen was similarly low, averaging 0.7%. Ash averaged about 7%.

The contribution of these organic and inorganic substances to the caloric value of sardine ovaries is negligible.

The similarity in quality and quantity of the major organic constituents in ripe ovarian tissue and larval yolk justifies caloric measurements of ripe ovaries to be applied to larval yolk. The caloric content of sardine ovarian yolk was found to average 5386 calories per gram dry weight.

Lasker and Theilacker (1962a) have shown that swimming and embryonic development are the two major factors influencing oxygen consumption in embryonic and larval sardines provided that temperature is constant. The average rates and their standard deviations for oxygen consumption by 33 individual embryos and larvae over the yolk-sac period are presented in Table II. By summing the mean rates over each time interval an overall sum of microliters of oxygen consumed per animal per 180-hour yolk-sac period is obtained. The caloric value of oxygen varies 7% for the full range of respiratory quotients associated with the utilization of protein, fat and carbohydrate (Swift and French, 1954), or 4690 to 5050 calories per liter of O_2 for R.Q.'s of 0.707 to 1.00. Therefore, 1 μl O_2 = 0.005 cal ±0.00035 cal, and the sardine embryo utilizes 0.063±0.0044 calories for catabolism during a 180-hour yolk-sac period.

TABLE II. Average oxygen consumption at 14°C by sardine embryos and larvae.

Number of animals	Time	QO_2	Standard deviation
7	0–42 hours	0.030	±0.0098
9	42–70 hours	0.066	±0.010
17	70–180 hours	0.088	±0.019

In Table III the catabolic requirements of sardine embryos and larvae are presented as they change with time. Yolk uptake is plotted as a volume decrease

TABLE III. Average yolk utilization by sardine embryos and larvae at 14°C expressed as diminishing volume and caloric uptake. The catabolic calories are based on the mean respiratory figures given in Table II. A calculation for percentage efficiency of yolk conversion to tissue is included below.

Elapsed hours from spawning	Yolk volume (mm^3)	Calories remaining	Catabolic calories
0	0.56	0.300	0
42	0.48	0.260	0.0063
71	0.29	0.160	0.0096
80	0.25	0.130	0.0040
100	0.16	0.085	0.0088
120	0.09	0.048	0.0088
140	0.04	0.021	0.0088
160	0.01	0.005	0.0088
180	0	0	0.0088
		Total =	0.064

$$\text{Percentage efficiency} = 100 \times \frac{0.300-0.064}{0.30} = 78.7\%$$

in Fig. 1 and presented as caloric utilization in Table III. No eggs were taken at precisely the time they were spawned, but at 20 hours after spawning there had been very little embryonic development and yolk uptake (Ahlstrom, 1943). It is assumed therefore that the volumes at 20 hours do not differ significantly from those at spawning. After this time the yolk is used at a rapid rate until it is finally completely consumed. It can be seen in Table III that the larvae have enough yolk during almost the entire yolk-sac period to provide for both catabolism and anabolism. After 160 hours there is only enough yolk to provide for somewhat less than is needed for respiratory requirements, and during this period the animal is on a deficit. This deficit appears to be made up by resorption of tissue.

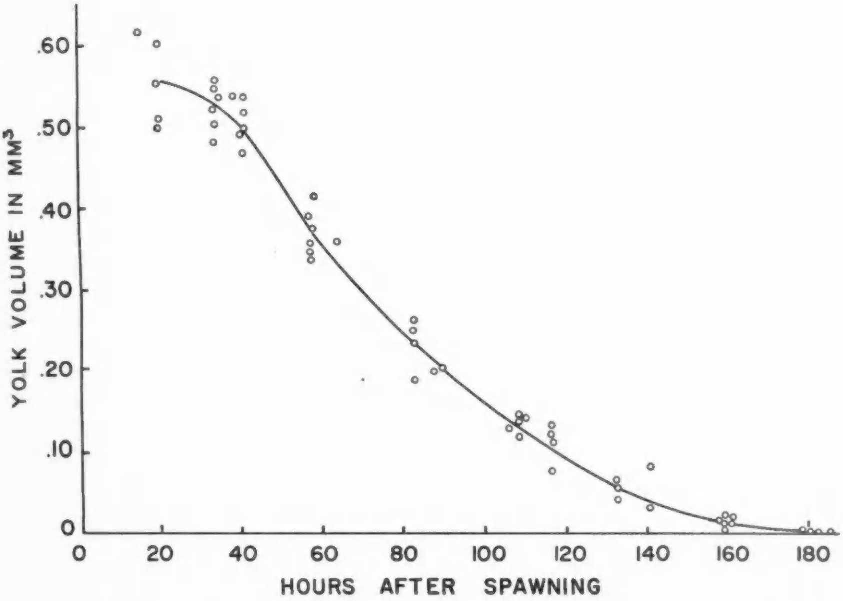

FIG. 1. Change in larval sardine yolk volume with time at 14°C. Each dot represents a different larva. Hatching occurred at 78 hours after spawning. The curve is plotted through average values at each time interval.

The gravimetric determinations of individual larval sardine weights with time are given in Fig. 2. Weight loss does not become evident until about 240 hours post-spawning. A line indicating the calculated average weight loss with time (0.081 microgram/larva/hour) is superimposed on the individual larval weights. There is a reasonably good agreement between the observed weights and the calculated weights after the larvae are 240 hours old. The weights plotted from 80 hours through 200 hours do not follow the projected slope closely. This is probably due to the variability of individual larvae in their swimming

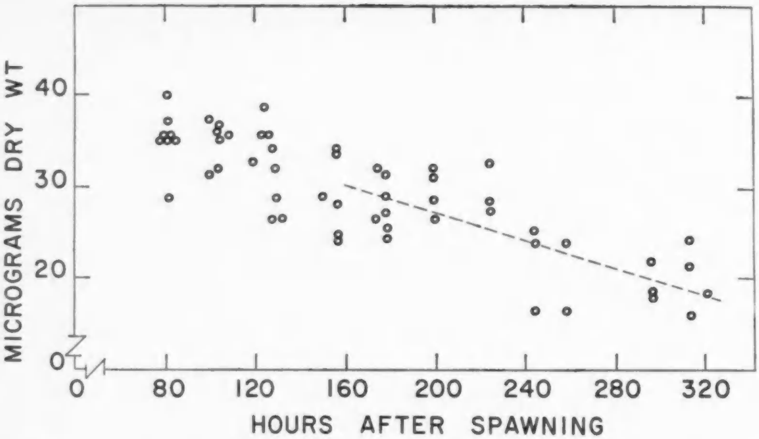

FIG. 2. Dry weights of individual sardine larvae after hatching. The oblique line represents the calculated weight loss due to catabolism.

activity. Larvae swimming actively and for sustained periods would catabolize and lose weight at a higher than average rate. Quiescent larvae would resorb less tissue per unit time.

Catabolism accounted for by respiration amounts to 21% of the caloric requirement over the entire yolk-sac period when calculated on the basis of 0.56 mm^3 yolk volume. The remainder (79%) is that which goes into the growth of the larva and the fraction due to excreted nitrogenous materials. Ivlev (1939) showed that the energy of waste products produced during the yolk-sac stage of the sheatfish, *Silurus glanis*, is very small, amounting to only 2% of the total energy available in the yolk. I analyzed for total nitrogen sardine eggs and larvae approximately 20 and 100 hours after spawning, respectively (Table IV). The loss of nitrogen due to excretion is so small that it could not be detected by the method used. Loss in energy due to excretion appears to be of the same order of magnitude as reported by Ivlev. For the smallest initial yolk volume measured, 0.50 mm^3, 23% would go for catabolism and 77% into growth. Smith (1947, 1952, 1957) and Hollett and Hayes (1946) found respectively a 60.2% efficiency for the trout (*Salmo irideus*) and 41% for the Atlantic salmon (*Salmo salar*) during development, by calculating from chemical analyses of the yolk using standard conversion factors for protein, fat and carbohydrate. Ivlev (1939) calculated an overall efficiency of 66% for the yolk-sac stage of the sheatfish.

TABLE IV. Total nitrogen of Pacific sardine eggs and larvae.

Number of eggs or larvae	Hours after spawning	Wt. total N (mg)	N per egg or larva
201 eggs	20	0.801	0.00399
389 larvae	100	1.567	0.00403

DISCUSSION

In this paper the quantitative energetic relationship of yolk to the developing sardine embryo and larva has been determined. Chemical analyses of the yolk confirm, in general, what is known of the chemistry of other teleost egg yolks (Smith, 1957), i.e., that protein is the most important food reserve, lipids also contribute a large part of the energy available to the embryo, and carbohydrates are of lesser importance as energy reserves. It has been shown that sardine larvae begin to show signs of tissue resorption and subsequent weight loss after the yolk has been completely consumed. This is probably due to the continued catabolic activity of the animal when no food is available. Berner (1959) and Arthur (MS, 1956) have noticed respectively that most of the anchovy (*Engraulis mordax*) and Pacific sardine larvae obtained from plankton hauls are in poor condition and have resorbed their livers. Shrinkage of starving sardine larvae after yolk-sac absorption is evident from Farris's (1959) data. By examining gut contents of Pacific sardine larvae caught in plankton nets, Arthur (1956) concluded that feeding incidence is very low, rarely exceeding 15% and generally below 10%. These facts indicate that many sardine larvae are starving in nature.

Laboratory observations of the developing larval sardine indicate that the jaw is not functional when the animal begins its metabolic deficit, i.e. the time that catabolism exceeds the energy provided by the remaining yolk supply. At the same time the larva's eyes are not fully pigmented, and lack of vision also must be a problem. Active seeking and capture of food probably does not begin until a later, as yet undetermined, time. Thus, at 14°C yolk utilization proceeds for 160 hours, and all of the metabolic requirements of the developing larva are met. The jaw starts forming at this time, but the animal does not have enough yolk to meet its metabolic requirements and goes on a partial deficit until 180 hours. By this time the yolk is completely utilized, and the jaw has developed fully. The larva swims actively at this age but does not appear to pursue moving nauplii or other food particles. If the animal does not come upon a particle of food by chance to overcome its continuing metabolic deficit, it will die shortly after vital physiological functions are affected. Increased temperature would undoubtedly have an accelerating effect on this process.

SUMMARY

1. Chemical analysis of Pacific sardine (*Sardinops caerulea* Girard) ripe ovaries which are composed chiefly of yolk, shows that protein is the major nutrient, amounting to over 70% of the dry weight; lipids constitute about 13%. The average caloric value of the ripe ovary is 5386 calories per gram dry weight.

2. Chemical analysis of larval yolk gave similar qualitative and quantitative results as those obtained with ripe ovaries. Thus caloric values obtained with ripe ovaries can be used to describe changes occurring while yolk is being utilized by the larva.

3. The caloric content of a single 0.56 mm^3 sardine egg yolk, based on an average water content of 91.2%, is 0.30 calorie.

4. Yolk volume changes with time in the embryo and larva indicates that the calories provided by the yolk meet the metabolic needs of the animal at 14°C until 160 hours after spawning. From this time on the larva is on a continuing energy deficit.

5. Although the jaw begins to form at about 160 hours, it is not fully formed until 180 hours after spawning. The larva does not actively pursue food available to it in laboratory jars. Although larvae of this age can swim actively the pursuit and grasping of food does not appear to be developed as yet. Hence obtaining food may simply be a matter of chance meeting between mouth and food particle.

6. If the energy deficit continues, as in a starving larva, concomitant weight losses occur due to tissue resorption which finally result in death.

7. For the volume of yolk (0.5–0.6 mm^3) available to sardine embryos, the efficiency of yolk utilization (i.e. conversion of yolk to tissue) for the entire yolk-sac period ranges from 77 to 79%. Energy loss due to excretion of waste products is small and could not be measured with available techniques.

I wish to acknowledge the technical assistance of Mrs Gail Theilacker and Mr Gerald Sanger.

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Possible Effects of Passamaquoddy Power Project on Clams, Scallops and Shipworms in Canadian Waters[1,2]

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ABSTRACT

Only three molluscs in the Passamaquoddy region of the Bay of Fundy have economic significance. The annual soft-shell clam (*Mya arenaria*) production now at 4 million lb will drop 2 million and fishermen's earnings will drop to $100,000 because the area of clam flats in the High Pool will decrease 95%. Annual scallop (*Placopecten magellanicus*) production, now at 60,000 lb, will increase to about 90,000 lb and fishermen's earnings will increase to about $36,000 because reduced water exchange in the High Pool will favour survival of larvae and recruitment of scallop stocks. The shipworm (*Teredo navalis*), no problem now, will become an expensive pest in the Low and High Pools because higher water temperatures will encourage the build-up of heavy breeding populations.

INTRODUCTION

MOST MOLLUSCS are sedentary animals and must accommodate themselves to their surroundings or perish. Their activities generally show great dependence on environmental factors. There are, for instance, threshold temperatures for shell movement, feeding and spawning. And, above threshold levels, there are precise relationships between temperature and rates of these activities. It is therefore to be expected that molluscs in the Passamaquoddy (Quoddy) region of the Bay of Fundy (Fig. 1) will be markedly affected by such changes as will attend proposed damming and tidal power development. Trites (1961) has deduced the nature and extent of hydrographic changes and the forecasts made here are based on his deductions and on other information assembled during our studies.

There are many species of molluscs in Canadian parts of the region but few are of economic importance. Mean landings from 1937 to 1955 inclusive show that the soft-shell clam is the most important commercially. In recent years 4 million lb (whole weight) have been dug annually. The scallop has been second in commercial importance, with landings approximating 60,000 lb of meats (adductor muscles only) or 540,000 lb of whole scallops, valued at $24,000.

Soft-shell clams are eaten by commercially valuable bottom-feeding fishes like the winter flounder (Medcof and MacPhail, 1952) and so are scallops. Thus both have an indirect economic importance as well as their direct importance as marketable products. And Passamaquoddy Bay abounds in molluscs which have no direct economic importance. They are not marketed but several of

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them, for example *Yoldia*, are eaten by bottom fishes like haddock (Homans and Needler, 1944) and therefore have indirect economic importance. We know too little to predict how the indirect importance of any of these species will be affected by damming.

A few molluscs are classed as economic liabilities, actual or potential, and must be considered here. Shipworms, *Teredo navalis* and *Xylophaga dorsalis*, are probably the most important because they do so much damage to wooden structures.

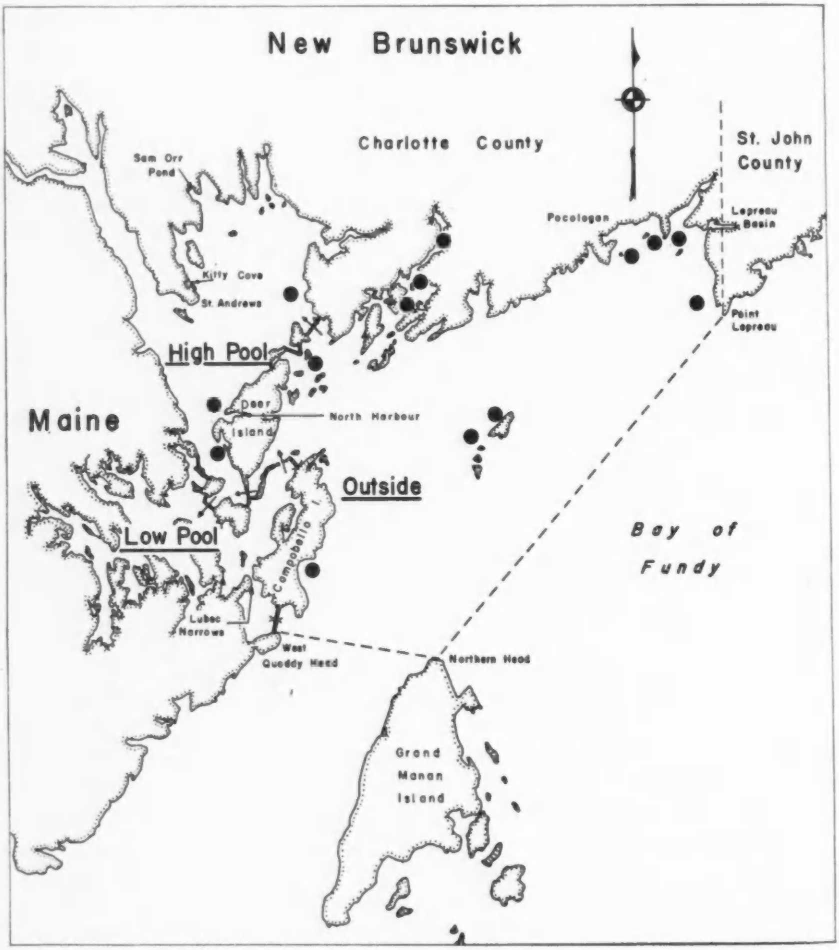
New Brunswick
Charlotte County
St. John County
Sam Orr Pond
Kitty Cove
St. Andrews
High Pool
Pocologan
Lepreau Basin
Point Lepreau
Maine
Deer Island
North Harbour
Outside
Low Pool
Campobello I.
Lubec Narrows
West Quoddy Head
Northern Head
Bay of Fundy
Grand Manan Island

FIG. 1. The broken line bounds the Quoddy region with its three major sub-divisions—High Pool (Passamaquoddy Bay), Low Pool (Cobscook Bay) and Outside. New Brunswick scallop fishing grounds are indicated by dots.

SOFT-SHELL CLAMS

Clam production has declined drastically in the past 10 years partly from green crab predation (MacPhail *et al.*, 1955) and partly from over-digging. But recently there has been a drastic fall-off in the numbers of green crabs, clam digging has been less intensive and clam stocks are showing signs of recovery. It is therefore reasonable to consider that the mean of the landings for the years 1937 to 1955 approximates the area's sustainable level of production under present conditions.

For purposes of this study it was necessary to re-allocate clam landings reported by the Department of Fisheries for Statistical Districts 51, 52 and 53 in terms of the three parts of the Quoddy region—High Pool, Low Pool and Outside (Fig. 1). Table I shows this re-allocation and also compares the present with predicted landings.

TABLE I. Present (mean for 1937 to 1955 inclusive) and predicted annual landings and landed values of soft-shell clams from various Canadian parts of the Quoddy region of the Bay of Fundy.

Area	Present			Predicted				
	High pool	Low pool	Outside	High pool		Low pool		Outside
				1st 10 years	Thereafter	1st 10 years	Thereafter	
Deer Island								
Pounds	52,300	0	0	0	2,600	0	0	0
Dollars	845	0	0	0	130	0	0	0
Campobello Island								
Pounds	0	17,300	8,700	0	103,000	9,000	19,000	8,700
Dollars	0	285	140	0	5,115	450	950	140
Mainland bordering Passamaquoddy Bay								
Pounds	2,063,000	0	0	0	103,000	0	0	0
Dollars	44,520	0	0	0	5,115	0	0	0
Mainland Outside								
Pounds	0	0	1,945,000	0	0	0	0	1,945,000
Dollars	0	0	45,100	0	0	0	0	97,685
Totals by areas								
Pounds	2,115,300	17,300	1,953,700	0	106,000	9,000	19,000	1,953,700
Dollars	45,365	285	45,240	0	5,300	450	950	98,000

	Present	Predicted	
Grand totals for Quoddy region		1st 10 years	Thereafter
Pounds	4,086,300	1,962,700	2,078,700
Value[a]	$204,315	$98,500	$103,950

[a]Based on the current price of 5 cents per pound. The 19-year average value is $90,890.

BASIS FOR PREDICTION

In the summer of 1958 the conditions on 4 clam flats in the region were studied to provide a basis for prediction. Two of these flats were inside and two outside Passamaquoddy Bay. A rectangular plot was laid out on each flat, its long axis parallel to shore and its shoreward boundary at high-water mark.

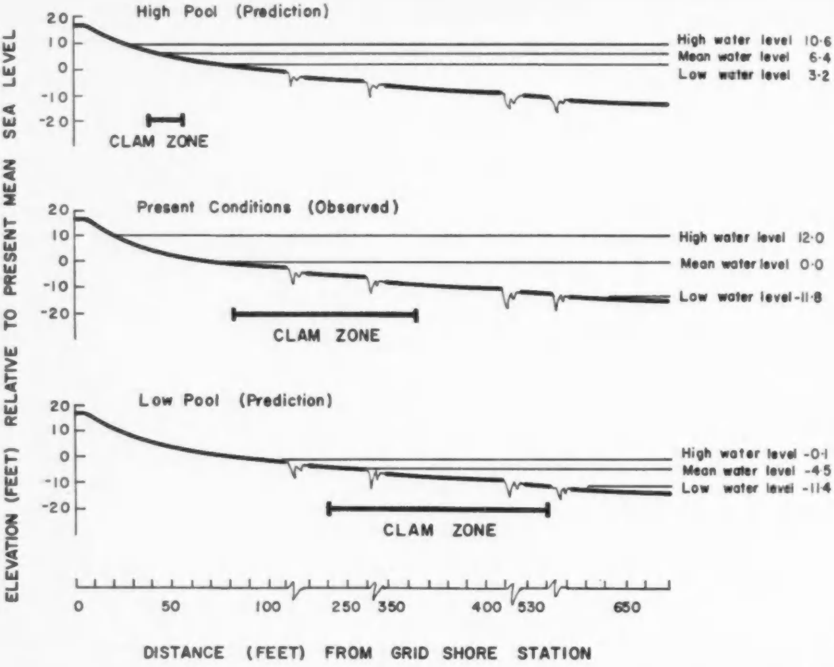

FIG. 2. Profile of a typical flat (St. Andrews habour) showing present and predicted positions of clam beds in High and Low Pools in relation to mean sea level and to highest high and lowest low water levels.

The first of the inside plots was on the St. Andrews harbour flat immediately west of the government wharf and measured 1,800 by 700 feet (550 by 215 m). It was contaminated with sewage, was not being harvested and therefore typified unharvested grounds in what will be either Low or High Pool areas. For comparison, the second plot, 1,800 by 1,000 feet (550 by 305 m) was marked out on the Pottery Bridge flat, one mile northwest of the first plot. It was being regularly harvested and typified exploited flats in what will be either Low or High Pool areas.

Of the two plots outside Passamaquoddy Bay, one, 1,200 feet by 600 feet (365 by 182 m) was on the Bridge flat in Lepreau Basin and the other, 1,200 feet by 800 feet (365 by 243 m) on the Slag flat in Pocologan Harbour.

Standard surveying equipment was used to mark off each plot with stakes in a grid pattern (usually in 100-foot squares) and to determine its elevation contours relative to mean sea level. A 1-square-foot sample of beach soil was dug at each grid stake, the soil character was noted and the clams more than 1 inch (25 mm) long were counted. From these counts the positions of beds (areas where clam counts exceeded 3 per square foot) were plotted along with data on elevation and soil composition.

The 4 areas studied are similar in contour and soil composition. Each has 3 clearly distinguishable sub-divisions. The first is inconspicuous. It is a narrow, horizontal ribbon of rocky beach close to high-water mark (Fig. 2). The second sub-division seaward from this first is a steep slope, usually of rock, shingle, coarse gravel or rocky mud which ends suddenly within 100 feet of high-water mark. The third sub-division is the flat proper, a nearly horizontal plane, sloping gently seaward to and beyond low-water mark. The soil in this sub-division is gravel-mud at the shoreward end, becoming more and more muddy with distance from shore. All clam beds are to be found within this third sub-division in a zone about 300 feet (91 m) wide which falls between levels corresponding to 1 foot above mean sea level and 6 to 7 feet below mean sea level (Fig. 2 and Table II). Thus, vertically the clam zone extends through roughly 30% of the total range of water levels at spring tides and occupies 50% of the flat exposed. The clam zone is bordered above and below by a ribbon of flat that is barren of clams.

TABLE II. Present conditions on the St. Andrews harbour clam flat (typical of Quoddy region) and predicted conditions in proposed High and Low Pool areas. All measurements are in feet and all heights, unless otherwise stated, refer to mean sea level.

	Present	Predicted	
		High pool	Low pool
Highest high water	12.0	10.6	−0.1
Lowest low water	−11.8	3.2	−11.4
Tidal range	23.8	7.4	11.3
Mean water level	0.0	6.4	−4.5
Shoreward boundary of clam zone, height	1.0	0.3	0.4
Seaward boundary of clam zone, height	−6.5	4.4	−7.6
Boundary-to-boundary height (linear) of clam zone	7.5	2.3	3.5
Linear height of clam zone as % of tidal range	31%	31%	31%
% of linear height of clam zone above mean water level	13%	13%	13%
Horizontal extent of clam zone	280	14	300
Horizontal extent of clam zone as % of present extent	100%	5%	110%

These findings are in general agreement with those reported by Newcombe (1935).

In predicting conditions that will result from damming, it is assumed that the new clam zone will bear proportionately the same relations to the new high- and the new low-water levels as the present clam zone in St. Andrews harbour bears to the present water levels. This means that vertically it will extend through 31% of the total new tidal range and that 13% of its extent will be above and 87% below the new mean water level (Table II; Fig. 3, 4). The predicted horizontal position and extent of each new clam zone is derived by projecting its vertical position as shown in Fig. 3 and 4 onto the bottom profile as defined in our study of existing conditions (Table II, Fig. 2).

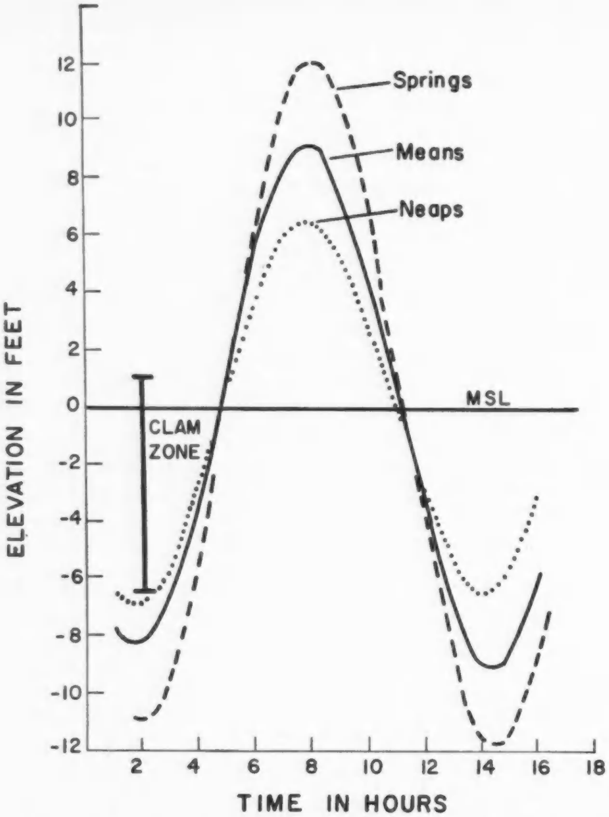

FIG. 3. Present vertical position and extent of St. Andrews harbour clam zone in relation to mean sea level and to water levels when the tide is in its neap, mean and spring phases (after Trites 1961).

Figure 4 shows that the nature of the tides will be quite different from those we have now (Fig. 3). For example, there will be almost no overlapping of levels between spring and neap tides in the High Pool. This means that quite different ribbons of beach will be exposed while the tide is in these two phases of its cycles. It is difficult to judge how this will affect the reliability of our predictions of production changes. But it is worth stating that the predicted High Pool conditions, both of tide and of clam distribution, approximately describe those now extant in Malpeque Bay near the Biological Sub-Station, Ellerslie, P.E.I., where clam production is very low.

The reliability of our forecasts is also limited by our lack of understanding of how changed Low and High Pool conditions will alter the present abundance and behaviour of clam predators such as the green crab and the winter flounder. We are therefore obliged to disregard them, which is equivalent to assuming that their changes will be mutually confounding. We must admit that this and several other assumptions made here are tenuous and that these forecasts of clam production, which we have been asked to make, cannot be regarded as firm predictions. They should be taken, as the title of this paper suggests, as our best opinions.

We likewise know too little about total plankton of the Quoddy region to venture opinions on how it will change and how possible changes in this food supply will affect survival, growth and commercial production of clams (and scallops). However, we can forecast for one plankter, *Gonyaulax*, which is responsible for paralytic shellfish poison problems.

For many years now the safe marketing of soft-shell clams from the Quoddy region has required special fishery regulations because of the seasonal appearance

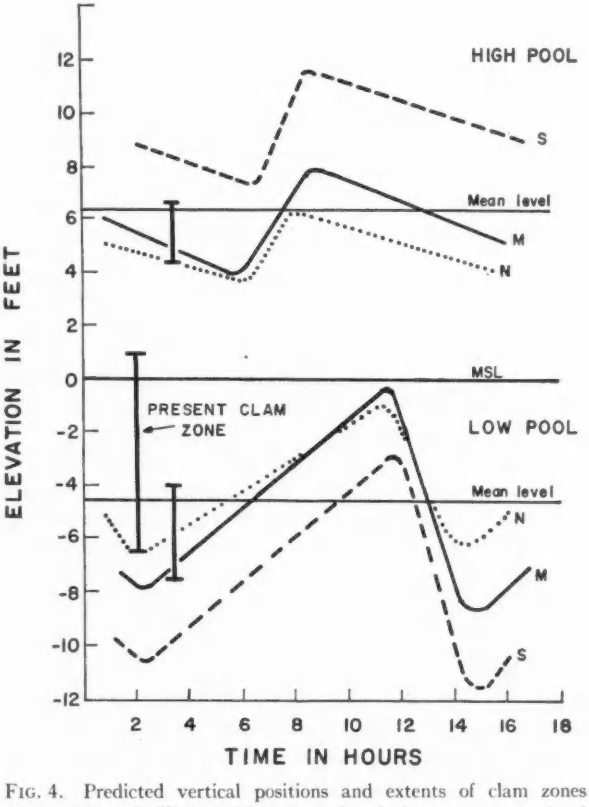

FIG. 4. Predicted vertical positions and extents of clam zones (vertical bars) in High and Low Pools in relation to mean sea level and to predicted water levels when the tide is in its neap, mean and spring phases. The position of the present clam zone, as in Figure 3, is shown here for comparison with the new positions (after Trites 1961).

of paralytic poison (Medcof *et al.*, 1947). These regulations do not seem to have affected total clam production because the stocks have been fully exploited in the safe open seasons. Actually, the waters of what will be the High and Low Pool have always been relatively safe. We believe their estuarial characteristics are responsible for the observed rarity of the dinoflagellate, *Gonyaulax*, on which the clams feed. Trites (1961) predicts that damming will exaggerate these estuarial characteristics and this should, if anything, decrease the poisoning risk in the High and Low Pool.

The risks of poisoning from consumption of clams (scallops are not involved) have been limited almost entirely to the Outside area and Trites predicts little change there. Thus, damming will not likely involve changes either in the pattern of paralytic shellfish poison hazards in the Quoddy region or in the commercial production of clams from the affected areas.

High Pool Prediction

Figures 2 and 4 show that present clam beds will be permanently submerged and unfishable when the High Pool is formed. These beds will soon die or disappear eventually through senescence because seed clams do not settle and grow below low-water mark in the Bay of Fundy.

The new clam zone will be narrow and occupy the steeply sloping landward part (second sub-division, Fig. 2) of the flat. We assume that its productive capacity per unit area will be the same as that of present flats. This is to say that production will be reduced in proportion to the reduction in area of flat, i.e., to 5% of present production (Table I). There are no clams now in what will be the new clam zone. Thus, when the High Pool is created, clam production from Passamaquoddy Bay will cease completely and instantly.

Most of our marketable clams are 6 to 8 years old (Newcombe, 1935) so the period of no production will be at least 6 to 8 years and probably 10 years because natural stocking of new ground is a gradual process. Indeed, it may be even longer because right now the soil in what will be the new clam zone is too coarse for clams to inhabit. There will have to be some resorting of sediments by wave action to produce muddy or sandy soils before clams can begin to populate this part of the flat.

After 10 years, production may be expected to begin to climb to 106,000 lb (5% of present volume) which at today's price will fetch fishermen $5,000 annually (Table I).

Low Pool Prediction

Figure 2 and Table II show that the extent of the Low Pool clam zone will be about the same (110%) as now, but its upper and lower boundaries will be 150 to 200 feet (46–61 m) further seaward. There will be an overlap of about 50% of new and old zones. Presumably production from the area of overlap will continue at its present level and clams will die out in the upper half of the present zone because it will be too high for clam survival. But clams will establish themselves in a 150- to 200-foot ribbon of now barren beach below the present clam zone. It will probably be 10 years before this new part of the clam zone comes into production. Thus, when the Low Pool is created, its clam production will drop suddenly to 50% and stay at that level for 10 years. Thereafter, it may be expected to rise gradually to present or slightly higher (110%) levels of about 19,000 lb, which at present prices will fetch the fishermen about $950 annually (Table I).

OUTSIDE AREA PREDICTION

Clam landings in the Outside area of the Quoddy region will not be affected because the clam zone will be the same as it is at present (Table II). Annual production will continue at about 2 million lb and, at present prices, will fetch the fishermen about $100,000 (Table I).

QUODDY REGION AS A WHOLE PREDICTION

Damming will bring about a substantial reduction in clam production. For 10 years it will be about 48% of present landings with an annual loss of about $100,000 (Table I), but thereafter there will be a slight recovery to about 51% of present landings.

Most of the loss will be felt in mainland communities bordering Passamaquoddy Bay but the North Harbour district of Deer Island (Fig. 1) will be similarly affected. Clam fishermen of the Low Pool area of Campobello Island will suffer a temporary loss but in the long run they will benefit slightly.

SCALLOPS

The scallop is the only mollusc besides the soft-shell clam that is harvested from Canadian parts of the Quoddy region in amounts sufficient to warrant consideration. Mean annual productions from various parts of the region in the period 1937 to 1955 inclusive are shown in Table III.

HIGH POOL PREDICTION

Scallops are deep-water forms and, unlike clams, will not be affected by changes in water level. However, predicted reductions in current speeds in Passamaquoddy Bay will favour silting, and, since scallops thrive best on a clean bottom, this change will make the Bay as a whole less suitable for scallops (Posgay, 1950; Yamamoto, 1960). It is doubtful, however, that the present principal scallop beds will be much affected because they are situated in the paths of currents that will lead from the inlet gates to the turbines (Fig. 1) where silting will be least.

Summer water temperatures in the High Pool will be higher than now (Trites, 1961). This will hasten development of larvae and will reduce the period during which they are subject to predation and will increase recruitment. On the other hand, high temperature will retard growth and reduce the meat yields of marketable scallops to levels approaching those in Northumberland Strait (Medcof, 1949; Chiasson, MS, 1949). The favourable and unfavourable effects of the higher temperatures will probably cancel one another and no allowance is made for them in predictions in Table III.

TABLE III. Present (mean 1937–1955) and predicted annual landings (pounds of meat) and landed values of scallops for various Canadian parts of the Quoddy region.

Statistical district no.	Present			Predicted		
	High pool	Low pool	Outside	High pool	Low pool	Outside
51						
Deer Island						
Pounds	7,300	0	7,300	14,600	0	7,300
Dollars	2,770	0	2,770	5,840	0	2,920
Campobello Island						
Pounds	0	0	7,300	0	0	7,300
Dollars	0	0	2,770	0	0	2,920
52						
Pounds	21,900	0	0	43,800	0	0
Dollars	8,910	0	0	17,520	0	0
53						
Pounds	0	0	16,000	0	0	16,000
Dollars	0	0	7,240	0	0	6,400
Totals by areas						
Pounds	29,200	0	30,600	58,400	0	30,600
Dollars	11,680	0	12,780	23,360	0	12,240
Totals for Quoddy region		*Present*			*Predicted*	
Pounds (19-year av.)		59,800			89,000	
Dollars (current value 40c lb)		23,920			35,600	

There is little basis for judging how scallop enemies will be affected by changed conditions. Some bottom-feeding fishes like haddock that eat scallops may be less abundant (McCracken, 1960), but higher temperatures may favour abundance of such enemies as starfish. Thus, differential effects on predator species will also likely cancel one another and we have not considered predators in making predictions.

However, we do think that reduced water exchange between Passamaquoddy Bay and the Bay of Fundy will affect scallop stocks. In considering this matter we have assumed, as is often assumed, that scallop beds are self-sustaining; that is, the larvae that settle on any bed are largely the progeny of scallops that live there. At the same time it is known that planktonic molluscan larvae may be carried far from their native areas by tidal currents. From studies of Bay of Fundy scallops, Dickie (1955) has concluded that recruitment and population size vary inversely with the rate of water exchange. The reliability of these assumptions and deductions determines the reliability of our predictions for the Quoddy region.

The water exchange between Passamaquoddy Bay (High Pool) and the Bay of Fundy will be reduced by 50%. Following Dickie, we therefore expect that loss of larvae from the High Pool will be reduced to half and that scallop production will be doubled (Table III). Fishermen's annual earnings should increase by about $12,000.

LOW POOL PREDICTION

Scallop production in this area is insignificant. It will remain insignificant because water exchange rates will increase. There is a chance that small beds will develop between Campobello and Deer Island in the approaches to the inflow and outflow gates where the bottom will be kept clean by tidal action.

Summer temperatures in the Low Pool will be higher than now. While this might favour heavier settlements of larvae, it is unlikely to offset the adverse effects of the greater water exchange. That part of the Low Pool which is south of Lubec Narrows may become too shallow and muddy to support scallops and summer temperatures may be too high.

The net effect of all these interacting factors on Low Pool scallop production is likely to be slight and no allowance is made for them in our predictions (Table III).

OUTSIDE AREA PREDICTION

The Outside area will not be greatly affected but small fishable beds may develop in the path of the High Pool intake and the Low Pool outflow. These benefits will be so slight that no allowance is made for them in predictions.

QUODDY REGION AS A WHOLE PREDICTION

Scallop production will improve in the High Pool and produce an overall increase of about 50% in landings. This will improve fishermen's earnings by about $12,000 annually (Table III). In general these predictions agree with those made by Dow and Baird (1960).

SHIPWORMS

For Canadian parts of the Quoddy region as a whole shipworms do not now constitute a problem but they do cause damage at times in limited areas which have high summer water temperatures. For example, in Kitty Cove, St. Andrews, N.B., wooden parts of floats maintained for swimmers are attacked periodically. Discarded frames found beached there in 1958 were completely riddled with tunnels very much like those made by *Teredo navalis*. Thus, even though no living animals have been found, it seems certain that this species is present. And in Sam Orr Pond, a warm-water branch of Birch Cove, tributary to Passamaquoddy Bay, teredinid larvae were found in plankton tows made in 1957 and 1958. There, too, no adults were found for species determination, but we suspect the larvae were those of *Teredo navalis*. There is a 1913 record of this species from Passamaquoddy Bay in weir poles (M'Gonigle, 1925). It is therefore not surprising to find evidence of it in the Quoddy region now.

Another shipworm, *Xylophaga*, is reported from Maine waters (Dow and Baird, 1953) and from Canadian waters (Whiteaves, 1901). But we have not observed it in the Quoddy region, nor have we found wood borings that we attribute to it.

High and Low Pools Prediction

The predicted oceanographic changes in the Quoddy region will affect *Teredo*. Reduced turbidity, which may be expected to accompany reduced current speeds (Trites, 1961), will favour growth of adults (Kindle, 1918); and reduced water exchange between Passamaquoddy Bay and the Bay of Fundy will favour retention of larvae within Passamaquoddy and their dense settlement on suitable substrates in the High Pool.

But the most important single factor affecting *Teredo* will be the rise in water temperature. The threshold temperature for spawning of *Teredo* is 16°C (Nelson, 1928) and summer temperatures in the High and Low Pools will approach 20°C. This will approximate conditions in Malpeque Bay (Needler and Needler, 1940) where shipworms thrive and regularly cause severe damage. The species will spread from its present foci, in places like Kitty Cove, and will build up dense breeding populations in both pools. These will be a menace to all wooden structures exposed to sea water, wharves, boats, weirs and lobster traps. Economically, *Teredo* will probably become the area's most important mollusc—important because it will be so destructive.

Outside Area Prediction

The heavy breeding populations of shipworms in the High and Low Pools will increase the numbers of larvae that will escape to the Outside area. Some of these will settle and cause damage to wooden structures near the outfall but the Outside area as a whole will not be affected because its low temperatures will discourage the activity of shipworms that settle there and will prevent them from spawning. However, wooden boats from the Outside and elsewhere will require extra protection if they frequent the High and Low Pools in summer months.

Quoddy Region as a Whole Prediction

We have no basis for predicting the extent of annual losses that will attend the spread of *Teredo*. There will be heavy costs for protective treatment of wooden structures. Boat bottoms, mooring buoys and wooden spar buoys used in navigation will have to be painted and renewed more frequently; lobster traps may have to be tarred and all wharves will have to be constructed of creosoted timber. If sardine weirs continue to be used after damming, annual repair costs will soar. In years following heavy settlements of shipworm larvae, weirs may have to be completely rebuilt.

Costs of combatting shipworms could easily equal or exceed the value of all the fisheries of the Quoddy region.

ACKNOWLEDGMENTS

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Lord worked up the statistical records of all shellfish landings, and Dr R. Trites provided background information on the oceanographic changes likely to attend damming. I would also thank Department of Fisheries agents: Mr W. F. Doucet, former Chief, Economics Branch, Halifax, N.S., supplied landings records and Mr G. E. Eldridge, Fisheries Officer, St. Andrews, N.B., assisted in interpreting these records.

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Record of the Blue Ling, *Molva byrkelange* (Walbaum), from the Newfoundland Area[1]

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ABSTRACT

A female specimen of European ling, 115 cm long, caught in Hermitage Bay, Nfld., Lat. 47°33'N, Long. 56°06'W on September 17, 1959, has been identified as the blue ling, *Molva byrkelange* (Walbaum). This is apparently the first record of this species from the western Atlantic west or south of West Greenland.

INTRODUCTION

On September 17, 1959 a 115-cm spent female specimen of the blue ling, *Molva byrkelange* (Walbaum), was caught by the Newfoundland otter-trawler *Pennyworth* while fishing for redfish in 130 fathoms (240 m) at the mouth of Hermitage Bay on the south coast of Newfoundland, Lat. 47°33'N, Long. 56°06'W. This fish (Fig. 1) was brought to the St. John's Station in good condition by the *Marinus*, research vessel of the Station, which was also operating in the Hermitage Bay area. At the Station it was preserved in 10% formalin and later examined by the authors.

DESCRIPTION

Round weight (in 10% formalin)	3.8 kg
Total length (fresh)	115 cm
Total length (in formalin)	112.1 cm
Standard length (snout to end of hypural)	104.7 cm
Head length (a)—measured directly on the fish	23.5 cm
Head length (b)—horizontal distance between planes	21.5 cm
Lower jaw protrusion beyond upper	0.5 cm
Longitudinal diameter of orbit	5.1 cm
Vertical diameter of orbit	4.5 cm
Interorbital (a) (least fleshy width)	2.9 cm
Interorbital (b) (least bony width)	2.1 cm

Other measurements and meristic counts are given in Table I. Our specimen lacked a barbel: only a small protuberance remained. The ventral fins ended 5.9 cm anterior to the posterior tip of the pectorals. The colour of the back was greyish or grey-brown. There was a black edge on the posterior fringe of the 2nd dorsal and anal fins.

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DISTRIBUTION OF THE THREE EUROPEAN SPECIES OF LING

Because this is apparently the first specimen of *Molva byrkelange* to be caught in the western Atlantic west or south of West Greenland it is worth while to establish its identity beyond reasonable doubt. Consequently we have discussed the distribution of the 3 European species of *Molva* and presented in Table 1 comparative data on our specimen and on these 3 species.

THE COMMON LING. The common ling, *Molva molva* (L.), is found in the eastern Atlantic from northern Norway and Iceland to the Bay of Biscay [9] and Morocco [2]. It is common in the Icelandic area, particularly in the warmer parts [7], but this is its farthest appearance westward [10], except for one specimen caught on the southwestern Grand Bank in February 1953 [11].

THE BLUE LING. The blue ling, *Molva byrkelange* (Walbaum), is a northerly form occurring in deep water from Finmark, the Faroes and Iceland to the Kattegat [8]. It inhabits deeper water than *M. molva* [2]. It is not uncommon in deep water S and W of Iceland but is very rare on the N and E coasts [7]. Tåning [10] points out that the 2 specimens of ling recorded from West Greenland by Jensen [3] as *M. molva* are really *M. byrkelange* (D_1, 12 and 14; D_2, 72 and 78; A, 69 and 74; P, 20, and 18 and 20; V, 7, and 6 and 7; vertebrae, 75 and 77). He therefore shows the range of this species as extending westward to southwestern Greenland. Jensen's specimens, in fact, are very much like our own Hermitage Bay specimen in their meristic characters and very likely the Hermitage Bay specimen came from Iceland, probably by way of Greenland.

Kotthaus and Krefft [5] record the capture of 76 *Molva byrkelange* 31–117 cm long, and 9 *Molva molva* by the *Anton Dohrn* otter-trawling surveys in deep water (150–500 m) on the Icelandic Shelf, off the S, SW, W and NW coasts of Iceland. They also record 11 *M. byrkelange* 84–108 cm long in one set at 375 m on the western part of the Anton Dohrn Bank off the east coast of Greenland, and 1 *M. byrkelange* 77 cm long at 250–300 m from Little Hellefiske Bank on the west coast of Greenland. Rahardjo [6] gives an account of *M. byrkelange* and *M. molva* caught from Iceland to Norway in the *Anton Dohrn* cruises of 1955-1957, and of these 2 species of ling from the same area landed during the same years at the Kiel fish market. The distribution of *M. molva* was from <150 to 350 m; that of *M. byrkelange* was from <150 to >500 m. The length of *M. molva* was up to about 180 cm and of *M. byrkelange* to about 150 cm.

The fin-ray and vertebral counts of the blue ling from Iceland were higher than of those from northern Norway.

Joensen [4] reports the capture of about 50 *M. byrkelange* on the W. Greenland banks by the Faroese trawler *Skalaberg*, with fisheries research personnel on board, from April 30-May 15, 1959.

THE SPANISH LING. The Spanish ling, *Molva macrophthalma* (Rafinesque), is found in the Mediterranean and in the deep water SW of Ireland (d'Ancona, [1]). (This species is more often referred to as *Molva elongata* (Risso), but the present name is used by Fraser-Brunner and Palmer [2].) Tåning [10, fig. 2]

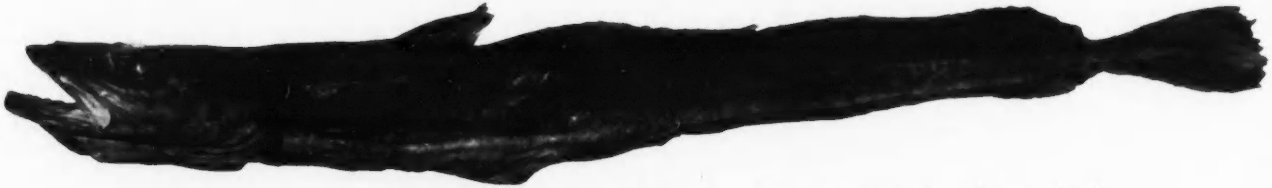

FIG. 1. Blue ling, *Molva byrkelange*, 115-cm ♀, caught at the mouth of Hermitage Bay, Newfoundland, on Sept. 17, 1959.

shows this species as extending from the northern shores of the Mediterranean, on both European and African coasts near the entrance to the Mediterranean and northwards to the west of Ireland and Scotland to beyond 60°N. Apparently it has not yet been recorded farther to the north or west, although Fraser-Brunner and Palmer [2] believe that its northward limits have been somewhat concealed by some misidentification of this species as *byrkelange*.

COMPARISON OF THE HERMITAGE BAY LING WITH THE THREE EUROPEAN SPECIES

Table I shows that the meristic characters alone, and especially the vertebral number, of the Hermitage Bay specimen are enough to separate it distinctly from *Molva molva*. Additional evidence that the specimen is not *M. molva* is to be found in the length of the base of the first dorsal compared with that of the second dorsal, the height of the first dorsal compared with that of the second, and the interorbital width in length of head.

TABLE I. Comparative information on the Hermitage Bay specimen of *Molva* and on the 3 European species of this genus. Data from authors as numbered in the list of references, p. 894.

Character	*Molva macrophthalma*		Hermitage Bay specimen	*Molva byrkelange*			*Molva molva*		
	[1]	[2]		[8]	[2]	[6]	[9]	[2]	[6]
1. Total length (fresh), cm	up to 90	...	115	...	to 150	146–150	to 200	...	171–175
2. Length of head in length of fish	5.5–6.5	5.0–5.9	4.8[a]	...	4.5–4.9	...	5.2–5.4	4.3–4.6	...
3. Interorbital width in length of head	...	9.0–11.1	8.1[b]	...	6.6–8.8	...	...	5.3–6.4	...
4. Diameter of eye in length of head	3.3–4.5	3.5–4.8	4.5[c]	...	3.5–4.9	...	...	4.7–5.8	...
5. First dorsal base in 2nd dorsal	...	9.2–11.0	6.6	...	5.3–7.5	...	...	3.5–4.5	...
6. Height 2nd dorsal in height 1st dorsal	>1	...	1.4[d]	>1	...	...	1.0	...	...
7. First dorsal rays	10–12	10–11 (rarely 12)	12	11–14	13–15	11–15	13–16	13–15	13–16
8. Second dorsal rays	77–82	74–82	73	74–83	72–76	69–80	60–70	59–64	57–69
9. Anal rays	70–79	73–79	68	70–81	71–73	62–75	57–66	56–59	55–67
10. Pectoral rays	18	15–18	20	18–20	18–20	...	18–21	18–20	...
11. Ventral rays	6	...	6	6	...	...	6	...	...
12. Vertebrae	...	...	77[e]	78	...	72–78	63–65	...	62–67

[a] Head length (a) and total length in formalin.
[b] Least fleshy interorbital width and head length (a).
[c] Longitudinal orbit diameter and head length (a).
[d] Greatest heights.
[e] Including urostylar half vertebra as 1 vertebra.

From the meristic characteristics, except for the pectoral rays, the Newfoundland specimen could be either *byrkelange* or *macrophthalma*. The number of pectoral rays, however, is beyond the *macrophthalma* range but within that of *byrkelange*. Both first dorsal and second dorsal rays also are a little closer in number to *byrkelange* than to *macrophthalma*.

The length of the Hermitage Bay specimen appears to be beyond the *macrophthalma* range and well within the *byrkelange* range. The length of the base of the first dorsal, compared with that of the second, definitely removes the Hermitage Bay specimen from the *macrophthalma* range but places it in the *byrkelange* range. The other body-proportion characteristics listed for the Hermitage Bay specimen in Table I are within the *byrkelange* range but usually outside the *macrophthalma* range.

As regards colour of the vertical fins, the description of our specimen agrees with Fraser-Brunner and Palmer's [2] description of *M. byrkelange* (which they say is identical, in respect to the colour of these fins, with *M. macrophthalma*—cf. also [1]). The Hermitage Bay fish was grey or grey-brown in body colour and lacked the marbling of the body colour found in *M. molva;* it also lacked that species' conspicuous and continuous white edge to the median fins, and the dark spot at the posterior edge of the 1st dorsal fin. Protrusion of the lower jaw beyond the upper, which is pronounced in our specimen, is not found in *M. molva* except in very large fish, whereas it appears in *M. byrkelange* as small as 60 cm and *M. macrophthalma* at least as small as 26 cm [2]. The short ventral fins ending anterior to the posterior tips of the pectorals distinguish our specimen from *M. macrophthalma*, which has the ventrals extending beyond the tips of the pectorals, whereas in the other two species they do not reach the tips of the pectorals [2].

There can be no doubt, therefore, that the Hermitage Bay specimen is *Molva byrkelange.*

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Flow of Water in the Passages of Passamaquoddy Bay Measured by the Electromagnetic Method[1,2]

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ABSTRACT

Water transports in the passages connecting Passamaquoddy Bay and the Bay of Fundy were measured by the electrical potential differences induced in the water moving across the earth's magnetic field. A phase difference between the transports in Letite and Western Passages was observed, slack water occurring later in Western Passage by 15 to 60 minutes. Variation of the transport with time for each passage was studied. A marked harmonic content was found, particularly of the second and third harmonics with periods six (6.2) and four (4.1) hours, and was evaluated by harmonic analysis.

The harmonic component content of the tidal current transports in the Saint Croix Estuary was found to be in close agreement with that of the observed tidal heights at St. Andrews, N.B. The harmonic content of the transports in Letite Passage and in Western Passage was related to hydraulic or frictional tidal flow and to shallow-water tides respectively. Currents in Letite Passage found at anchor Sta. 51 and deduced from the square root of the head measured by tide staffs were consistent in form and phase with data from the electrode voltages.

A small residual transport from Passamaquoddy Bay through Western Passage was inferred with some uncertainty.

INTRODUCTION

Water transport through the passages connecting Passamaquoddy Bay and the Bay of Fundy is an important element in the oceanography of the area. The study of this transport was one of the undertakings of the Research Committee of the International Passamaquoddy Fisheries Board in order to predict the effect of the proposed tidal power project on the fisheries in this area. Current measurements were made by a variety of means throughout the Passamaquoddy area. It was hoped that current measurements by the electromagnetic method might supplement the data from current meters, drift bottles, etc., and establish the value of this method in an area of strong tidal currents such as the Quoddy Region.

Passamaquoddy Bay is connected with the Bay of Fundy by Western Passage and Letite Passage (Fig. 1). Two additional minor passages, Little Letite and Doyle, connect the two bodies of water. Through these four passages, there is a transport in a tidal half-cycle (6.2 hours) varying from 35×10^9 ft^3 at neap tides

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[2] International Passamaquoddy Fisheries Board, 1956–59. Scientific Report No. 32.

[3] Present address: P.O. Box 444, Sackville, N.B.

[4] Essentially all of the investigation described in this report was conducted prior to the Fisheries Research Board of Canada moving the base of its Atlantic Oceanographic Group from the Board's Biological Station at St. Andrews, N.B., to Halifax, N.S.

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to 70 × 10^9 ft^3 at spring tides. Discharge of fresh water into Passamaquoddy Bay is of the order of 0.35 × 10^9 ft^3 per day, a quantity small compared to the tidal prism, and is unobservable in the present current measurements.

The comparison of the transports through the two larger passages, the variation of the currents in the tidal cycle, the residual flow if any, and the phase relations of currents in the two passages with the tidal data for the region, are the subjects of this report.

THE ELECTROMAGNETIC METHOD

Shortly after his discovery of the principle of electromagnetic induction, Faraday (1832) predicted that electrical potential differences would exist between the two sides of a moving stream of water, citing the Straits of Dover as an example. He attempted, unsuccessfully, to detect the effect by immersing copper plates in the two edges of the Thames River stream and measuring their potential difference. Later observers were more successful. Young *et al.* (1920) were the first to apply the method to the actual measurement of tidal streams. Since these modest beginnings, theory and technique have been developed by Longuet-Higgins (1949), by von Arx (1950) who modified the method to make current measurements using a moving ship equipped with a pair of towed electrodes, and by Bowden (1956) who investigated the flow of water through the Straits of Dover.

The physical and mathematical principles involved have been fully treated by Longuet-Higgins *et al.* (1954) and others and are included in this report in a brief form only.

When a stream of water moving with a velocity V cuts the vertical component of the earth's magnetic field H_z an electromotive force E is induced between two points on opposite sides of the stream a distance L apart. This electromotive force is given by the equation:

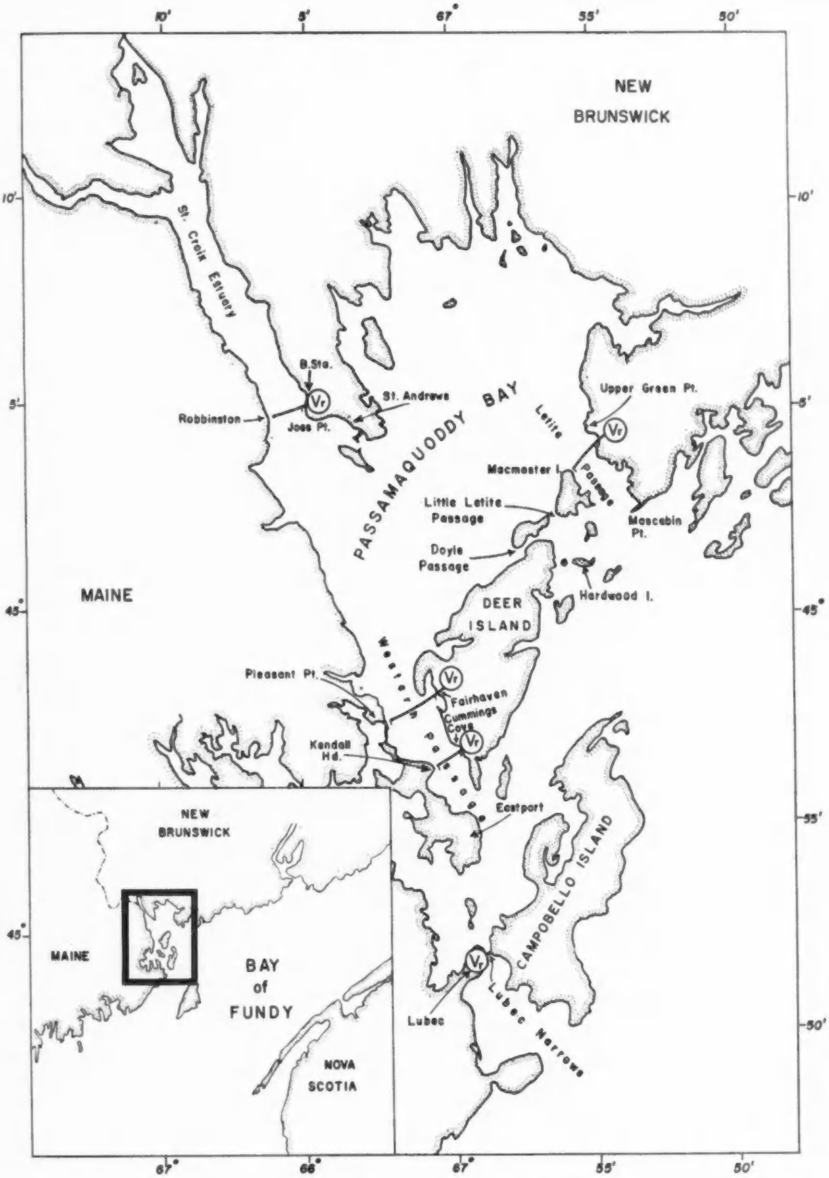
$$E = H_z \cdot L \cdot V \qquad \ldots (1)$$

provided the velocity is constant at all points and the boundaries of the channel are of non-conducting material. However the velocity distribution across a channel is rarely uniform. Malkus and Stern (1952) have shown that the electric potential developed by an ocean current is directly proportional to the total fluid transport. Therefore the electric potential developed across a channel will be directly proportional to the net transport (or to the mean velocity through the section).

In general the observed potential across a channel will be less than that given in Equation (1) due to the finite resistance of the bottom, and may be written:

$$E = \frac{1}{K} \cdot H_z \cdot L \cdot \bar{V} \qquad \ldots (2)$$

where K is a constant which is greater than unity, L the width of the channel and $\bar{V}$ the mean velocity through the section. The constant, K, can be given a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NEW BRUNSWICK
St. Croix Estuary
B.Sta.
Vr
Robbinston
Joes Pt.
St. Andrews
PASSAMAQUODDY BAY
Letite Passage
Upper Green Pt.
Macmaster I.
Little Letite Passage
Mascabin Pt.
Doyle Passage
Hardwood I.
MAINE
DEER ISLAND
Western Passage
Pleasant Pt.
Fairhaven
Cummings Cove
Kendall Hd.
Eastport
CAMPOBELLO ISLAND
Lubec
Lubec Narrows
NEW BRUNSWICK
MAINE
BAY of FUNDY
NOVA SCOTIA
45°
66°

Fig. 1. Passamaquoddy region showing location of installations.

theoretical interpretation in terms of the form and electrical resistance of the boundary material and the water mass. This subject has been extensively treated by Longuet-Higgins (1949) and Longuet-Higgins *et al.* (1954).

The constant K may be evaluated by measuring directly the flow of water through the section between the electrodes, using current meters. If, however, the installation is across the mouth of an embayment, approximate evaluation of K can be made from the known tidal transport.

Difficulties and uncertainties in the interpretation of the record of observed voltages arise from time to time owing to the presence of geomagnetic disturbances and earth currents as well as from some polarization of the electrodes. A turbulent stream over an irregular bottom doubtless gives rise to electrical signals because of the irregular vertical velocities interacting with the horizontal component of the earth's magnetic field.

APPARATUS

Electrical contact with the water was made through non-polarizing electrodes, silver-silver chloride, as used by von Arx (1950). Each electrode was mounted in a hollowed wooden block with vents to permit water to circulate. Glass wool was packed around the electrode which was joined to the cable by a soldered connection carefully insulated from the sea water. This electrode assembly was mounted on a wooden post set in a heavy concrete base which was lowered to the bed of the sea. An insulated cable laid on the sea bottom connected each electrode to the recording installation (Fig. 2).

The two electrodes were connected across two series resistances R_1 and R_2, each of a relatively high value. A Varian recorder (Model G-10) of sensitivity 50 millivolts for full-scale deflection measured the potential difference across R_1 only. This recorder operates on the potentiometer principle with automatic null-balancing. As no current flows through the input terminals of the recorder at null-balance, its apparent input resistance approaches infinity.

The potential difference between the electrodes in volts (E_e) is given in terms of the voltage at the recorder terminals (E_r), and the voltage divider resistors R_1 and R_2 by the equation:

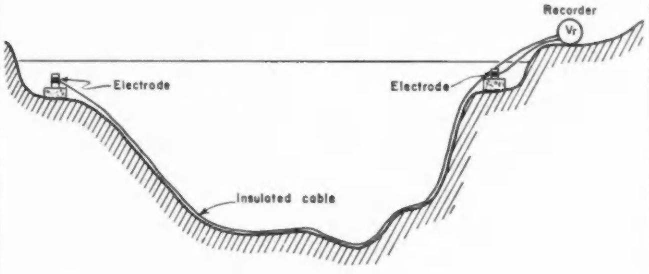
$$E_e = \frac{(R_1 + R_2)}{R_1} \cdot E_r = C \cdot E_r \qquad \ldots (3)$$

where C is the factor by which the recorder reading is multiplied to give the potential difference between the electrodes.

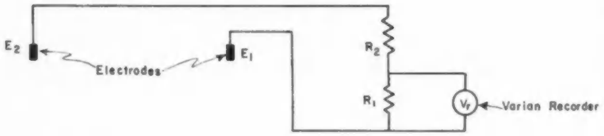
FIELD INSTALLATIONS

St. Croix Estuary, 1957

The apparatus was first used in July 1957, when an installation was placed across the St. Croix estuary near St. Andrews (Fig. 1). This installation permitted testing the type of cable and the technique of laying it, as well as an evaluation of the constant K, since the intertidal volume could be computed.



(a) SCHEMATIC CHANNEL CROSS SECTION



(b) SCHEMATIC DIAGRAM OF ELECTRICAL CIRCUIT

FIG. 2. Schematic diagram of (a) channel cross section with electrodes, cable, and recorder, and (b) electrical circuit.

An electrode was placed in the water 48 ft below mean sea level at Robbinston, Me., and a connecting cable laid to the pier at the Fisheries Research Board of Canada Biological Station, St. Andrews, N.B. The second electrode was placed in 19 ft of water near the pier. Depth measurements in feet (ft) are referred to mean sea level at Eastport, Me., throughout this report. The electrode separation was 5,550 ft. The mean depth of the section, as determined by an echo sounder, was 69 ft (Fig. 3-(a)).

The installation was removed after operating successfully for a period of 29 days.

WESTERN PASSAGE, 1957

In Western Passage electrodes were installed at Kendall Head, Me., and Cummings Cove, N.B., (Fig. 3-(b)) in 28 and 40 ft of water respectively on August 8. The cable remained intact for only a few hours; it was then accidentally severed by a fishing trawler operating in the area. A second cable was laid on August 15 and voltage measurements were recorded for 10 days, when the cable was parted near Kendall Head (cause unknown). Figure 3-(b) shows the cross-section of Western Passage and the location of the electrodes. The electrode separation was 4,560 ft and the mean depth of the section as determined by echo sounder was 117 ft.

LETITE PASSAGE, 1957

Attempts were made on several occasions to place a cable and electrodes in Letite Passage between Mascabin Point and Hardwood Island. The cable, a seven-strand copper conductor with a breaking strength of less than 200 lb, broke on each occasion as soon as the full force of the tidal stream struck it. It was assumed that the very irregular bottom kept short lengths of the cable suspended above the bottom. The project was eventually given up until a stronger cable could be procured.

LUBEC NARROWS, 1958

A New Brunswick Telephone Company cable from Lubec, Me., to Campobello Island was made available for use in Lubec Narrows. A recorder was installed at Lubec on March 12, with electrodes 13 ft below the surface and a separation of 760 ft (Fig. 3-(c)). The mean depth of the section was 33 ft. The installation was in operation from March 12 to May 23 and again for the period July 14–21.

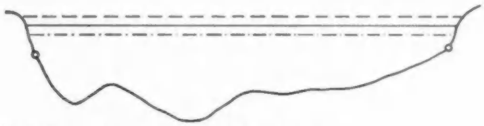
WESTERN PASSAGE AND LETITE PASSAGE, 1958

Recorder installations were re-established in Western Passage and Letite Passage using a heavier cable with a rated breaking stress of 1,230 lb. The locations used in 1957 were altered in each instance to a wider section of the passages, to reduce the stresses due to water currents on any suspended portions of the cable.

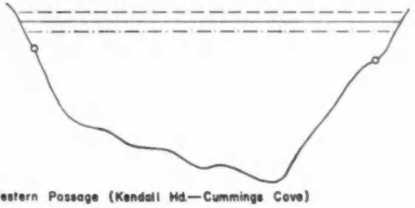
In Western Passage, the cable was laid from Pleasant Point, Me., to Fairhaven, Deer Island (Fig. 7). The electrode separation was 7,080 ft and the mean depth of the section determined by echo sounder was 167 ft (Fig. 3-(d)). The Pleasant Point electrode was placed in 28 ft of water and the Fairhaven one in 13 ft.

In Letite Passage, the electrodes were placed near the northeast point of McMaster Island, and at a point near the shore southeast of Upper Green Point (Fig. 8). Electrodes were respectively at depths 37 and 15 ft with a separation of 6,000 ft. The mean depth of the section (Fig. 3-(e)), determined by echo sounder, was 120 ft.

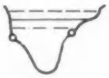
The Fairhaven installation was put in operation on June 10, and the one at Letite on June 13. The Letite recorder was maintained in operation until December 1958 and the Fairhaven recorder until May 1959. There were several interruptions in the records due to failure of the recording pen to ink the chart properly, lightning discharge, accidental breaking of a cable by the anchor of a fishing vessel, a leak in a water main causing a recorder damage, etc. No interruption lasted for more than 10 days.



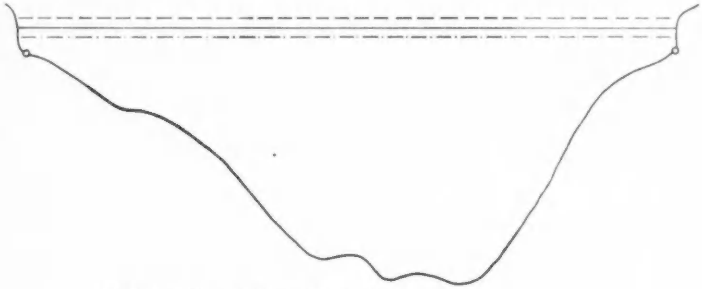
(a) St. Croix Estuary (Robbinston—Biological Station)



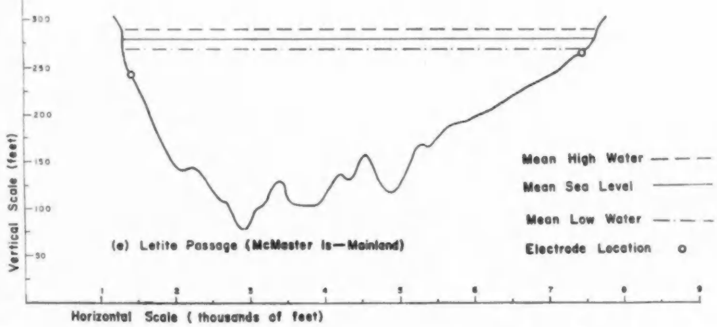
(b) Western Passage (Kendall Hd.—Cummings Cove)



(c) Lubec Narrows (Lubec—Campobello)



(d) Western Passage (Pleasant Pt.—Fairhaven)



(e) Letite Passage (McMaster Is—Mainland)

Vertical Scale (feet)
300
250
200
150
100
50
1
2
3
4
5
6
7
8
9
Horizontal Scale (thousands of feet)
Mean High Water
Mean Sea Level
Mean Low Water
Electrode Location

FIG. 3. Cross sections of passages and electrode locations.

St. Croix Estuary, 1960

Cables were again laid in the St. Croix estuary with one electrode at Robbinston, Me., and the other at the pier at the Biological Station (Fig. 1), as in 1957. A second installation was placed with electrodes at the pier and at a point in mid-river approximately half way to Robbinston. The intention was to investigate the water transport in the two halves of the river section. Difficulties with the operation of the installation were encountered and after a month the installation of the cable to Robbinston failed. The second installation extending across the eastern half of the estuary was in operation most of July and August. The records showed much irregularity, though in general the flood stream was much weaker than the ebb stream. No continuing and consistent pattern was found in the record though there were suggestions of an intermittent eddy system in this portion of the river where Joe's Point projects beyond Brandy Cove, the location of the Biological Station.

With the exception of the Lubec installation, a voltage divider combination was placed between the electrode leads and the recorder input. The resistances used and the multiplying factor, C, for each of the above installations are given in Table I.

Table I. The resistance values and multiplying factors used for each cable installation.

Location of recorder	Resistance $(R_1 + R_2)$ across electrodes	Resistance R_1 across recorder	Multiplying factor $C = \frac{R_1 + R_2}{R_1}$
	ohms	*ohms*	
St. Croix estuary, 1957	56,600	28,600	1.98
Western Passage, 1957	281,000	54,800	5.13
Lubec Narrows, 1958	No voltage divider used	–	1.00
Western Passage, 1958	168,000	35,200	4.77
Letite Passage, 1958	51,000	26,000	1.97

RESULTS AND DISCUSSION

St. Croix Estuary

The Varian recorder followed consistently the changing amplitudes of successive tidal streams from springs to neaps, and showed also the diurnal inequalities. The time of occurrence of zero potential difference corresponded closely with that of high and low water as measured at the Government Wharf in St. Andrews, as well as with the predicted times in the Tide Tables.

The mean tidal prism for the St. Croix estuary above the installation was calculated from the U.S. Coast and Geodetic Survey Chart No. 801 (1957) and the Atlantic Coast Tide and Current Tables (1957) and found to contain 7.3×10^9 ft³. The area of the section of the estuary between the electrodes was determined from an echo-sounder survey and found to be 3.86×10^5 ft². From these data a mean speed through the section was found to be 0.85 ft/sec taken over a half-tidal cycle. In turn the constant K of Equation (2) was calculated and found to be 1.2 for this location.

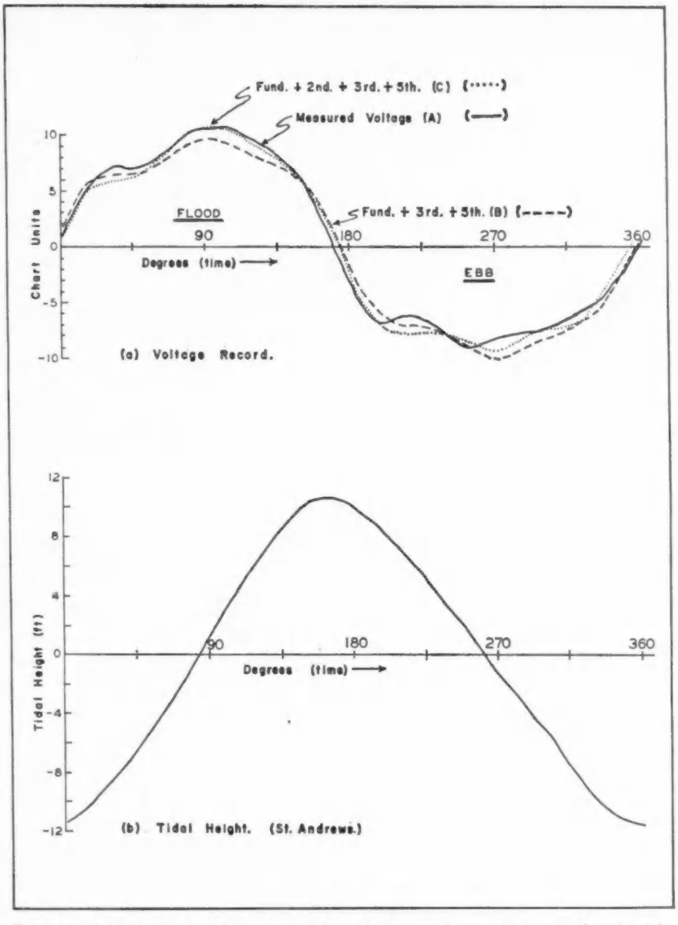


FIG. 4. (a) Typical voltage record and harmonic components for 12.4-hr tidal cycle, St. Croix estuary, and (b) tidal height at St. Andrews (12.4-hr cycle).

A typical voltage record for one tidal cycle (12.4 hr) is shown in Fig. 4-(a), Curve (A). This record is characteristic of both neap and spring tides. A striking feature of the curve is the plateau in the first half of both the flood and ebb streams, followed by a rise to the maximum.

Harmonic analyses of five 12.4-hr tidal cycles of voltage records were made using a twelve-ordinate schedule (Brooks and Carruthers, 1953) to give the amplitude and phase constant of the first five harmonic components n in the harmonic series, where Y = voltage amplitude, A_n = amplitude of the nth harmonic, Θ = time angle, and ϕ_n = phase angle of the nth harmonic:

$$Y = \sum_{n=1}^{\infty} A_n \sin (n\,\Theta + \phi_n) \qquad \ldots (4)$$

Mean values for the harmonic constants are given in Table II, columns under Section A. The amplitude of the fundamental harmonic is adjusted to an arbitrary one hundred units while the corresponding phase angle ϕ is adjusted to zero.

Harmonic analyses of heights were made of nine 12.4-hr tidal cycles, as recorded by the St. Andrews tide gauge. The mean values of the first five harmonic components are given in Table II, Section B, with the height and phase angle for the fundamental term (first harmonic) arbitrarily adjusted to one hundred units and -90° respectively. Differentiation of the tidal height with respect to time angle Θ yields terms proportional to the rate of transport into the estuary which are given in Table II, Section C. These values correspond with the relative voltage (transport) terms in Section A of the Table. The contribution of fresh water from river discharge is negligibly small compared to this.

TABLE II. Mean values of the harmonic constants of the tidal transport and amplitude in the St. Croix estuary for five tidal cycles.

Harmonic	**Section A** Voltage (transport) St. Croix estuary		**Section B** Tidal height St. Andrews		**Section C** Rate of change of tidal height St. Andrews	
n	A_n*	ϕ_n	A'_n	ϕ'_n	A''_n	ϕ''_n
1	100.0	0	100.0	−90	100.0	0
2	6.8	−101	3.7	−171	7.4	−81
3	12.8	+32	4.0	−68	12.0	+22
4	5.3	−54	0.9	−138	3.6	−48
5	6.2	+6	0.8	−63	4.0	+27

*Relative harmonic constants ($A_1 = 100$).

The large third harmonic component, approximately 13% of the fundamental, and also the second harmonic term of 7% of the fundamental are significant features of the transport in the estuary and are related to the conditions and currents in Letite Passage and Western Passage respectively, as will be shown later.

LUBEC NARROWS

The voltage recorder at Lubec varied erratically and its trace appeared to bear little relation to the water transports in the Narrows. Large disturbances, often at 24-hr intervals, occurred frequently. At other times the pen would shift abruptly to a new mean value. The power supply to the recorder was found to vary over wide limits and surges were frequent. Tests were made on the stability of the recorder sensitivity to supply voltage fluctuations by inserting a Variac in the supply mains and manually varying the supply from 90 to 130 volts with a period varying from approximately one second up to several minutes. Recorded input potentials remained steady under these conditions. The relative stability of the recorder suggested that for the most part the recorder was functioning properly and that the voltages recorded were actually developed across the electrodes.

Longuet-Higgins (1949) dealt theoretically with the distribution of potential gradients beyond the sides of a channel. Flow of water in a neighbouring channel of sufficient size may alter significantly the distribution of potential across the one under study. The larger flow of water into and out of Cobscook Bay immediately north of Lubec Narrows possibly accounts for some of the irregularity picked up by the installation. This was the only installation where it was considered likely that significant disturbance was present from neighbouring channels.

No systematic analysis of the records has been attempted because of the irregular variations in potential together with a very "noisy" record and evidence of a shifting zero.

LETITE PASSAGE AND WESTERN PASSAGE

GENERAL FEATURES

Potential differences recorded by the installations systematically followed the changing amplitudes of the tidal streams, both diurnally and from neaps to springs. For both passages the transport traces over a tidal cycle, as given by the voltage records, show a marked content of high-order harmonics, as shallow water tidal theory would predict (Pillsbury, 1939).

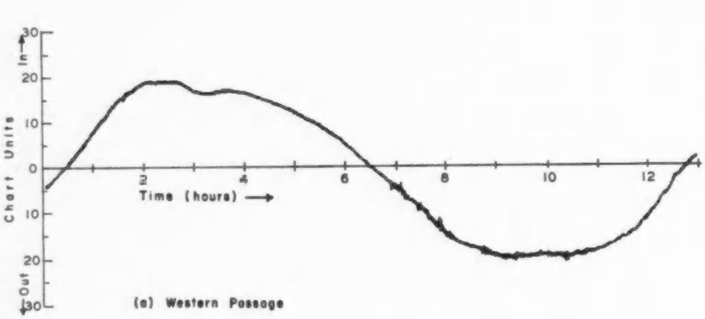
For these records difficulty and uncertainty arose in establishing the true zero for slack waters. If the instrument zero is used for one period in Letite Passage (latter part of July and early in August) there would be inferred ebb streams of duration approaching 7 hr and of velocities sometimes as great as 2½ times that of the flood streams. However, during the same period in Western Passage the velocities of ebb and flood and the half-tide intervals were nearly equal. It was felt that it was unrealistic to assume the instrument zero corresponded to slack water, and that there must be some dissimilarity in the electrodes or some interference such as earth currents which have proved to be a source of trouble for other workers in this field.

It was decided to make the assumption that the flood and ebb tide intervals in the passages correspond closely with the intervals for St. Andrews as taken from the Atlantic Coast Tide and Current Tables (1957). Intervals of this duration were then selected on the record so that the readings were the same at the beginning and end of the interval. These readings were then used to obtain a running mean zero to represent slack water.

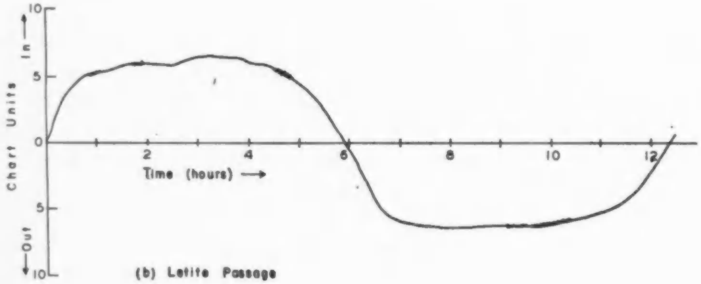
From the tidal amplitude curves at St. Andrews the rising and falling tides were found to differ in duration. The mean period from low to high water was found to be 6.0 hr, whereas the period from high to low water was 6.4 hr.

The shape and characteristics of the transport curves for the two passages were distinctly different. The Letite record was markedly flat-topped with a rapid increase in the first hour following slack water. Maximum transport was reached near half tide. The rate of change of the current (the slope of the voltage curve) was greater following slack water than before, for both flood and ebb stream. The signal was relatively free from "noise" although a brief period of "noise" usually appeared for about a quarter hour toward the end of the flood tide. A typical record for Letite Passage is reproduced in Fig. 5-(b).

In Western Passage, the transport rose less rapidly than in Letite, reaching its maximum in less than 3 hr, after which it decreased gradually to zero. This asymmetry occurred in both flood and ebb streams, but was more marked in the former. The record was generally "noisy" compared to the relatively "quiet" Letite record. A typical record for a tidal cycle for Western Passage is shown in Fig. 5-(a).



(a) Western Passage



(b) Letite Passage

FIG. 5. Typical voltage record, 12.4-hr tidal cycle, for Western and Letite Passages.

PHASE DIFFERENCES

The times of slack water in Letite and Western Passages, as determined from the voltage records, were found to differ. In all instances, slack water occurred later in Western Passage than in Letite Passage. Time differences in slack water between the two passages were plotted against time for a 6-month interval (Fig. 6) and a continuous curve drawn through the points. Time differences were found to vary from 15 minutes to values exceeding 60 minutes, with what appeared to be a degree of periodicity. Various factors such as tidal heights, phase of moon, etc. (Fig. 6), were considered in an attempt to find an explanation for these variations in phase difference, but without success.

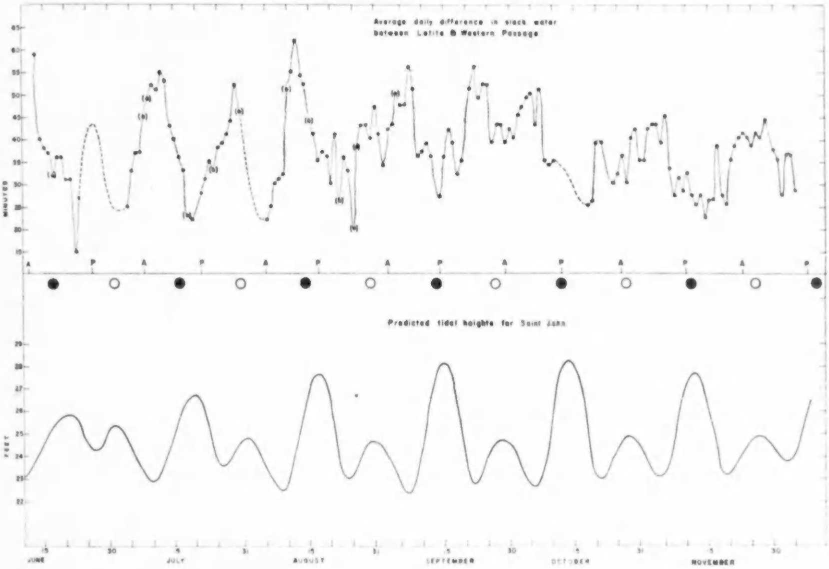


FIG. 6. Time difference of slack water for Letite and Western Passages for 6-month interval, June–November, 1958, corresponding tidal height at Saint John, and moon's phases.

HARMONIC ANALYSIS

Records for nine 12.4-hr tidal cycles of transports in Letite Passage and Western Passage as well as the corresponding tide gauge record for St. Andrews were subjected to harmonic analysis (Brooks and Carruthers, 1953) to obtain the constants for five harmonic components as in equation (4). These are given in Table III with the amplitude of the first harmonic (fundamental) arbitrarily adjusted to one hundred units. The phase angles for the first harmonic terms for Letite Passage and Western Passage are also adjusted to $+7^{\circ}$ and -7° corresponding to a time difference of approximately 30 minutes between slack water in these passages.

TABLE III. Mean values of the harmonic constants of the tidal transports in Letite and Western Passages, and the tidal amplitude at St. Andrews for nine tidal cycles.

Harmonic	Voltage (transport) Letite Passage		Voltage (transport) Western Passage		Tidal height St. Andrews		Rate of change tidal height St. Andrews	
n	A_n*	ϕ_n	A_n	ϕ_n	A'_n	ϕ'_n	A''_n	ϕ''_n
1	100.0	+7°	100.0	−7°	100.0	−90	100.0	0
2	7.2	−99°	12.4	−28°	3.7	−171	7.4	−81
3	19.4	+13°	8.7	−64°	4.0	−68	12.0	+22
4	3.7	−84°	3.6	−84°	0.9	−138	3.6	−48
5	5.1	−17°	2.0	−139°	0.8	−63	4.0	+27

*Relative harmonic constants ($A_1 = 100$).

The second harmonic amplitude is seen to be over 12% of the fundamental in Western Passage and 7% in Letite Passage. This would appear to be a shallow water tide component arising through the distortion of the tidal wave for which the velocity of the crest is greater than that of the wave trough (Doodson and Warburg, 1941).

The third harmonic amplitude is almost 20% in Letite Passage in contrast with 7% for the second harmonic term. Pillsbury (1939) refers to hydraulic or frictional tidal flow as that found in tidal straits of moderate depth subject to considerable tidal head in which the flow is determined by the square root of the head. Harris (1901) has shown that where the flow through a passage varies with the square root of the head a sinusoidal variation outside will result in a third harmonic term in the current through the passage. He refers to this as an overtide where the shallowness of the water is not responsible.

It thus seems that the conditions of flow in Western Passage and Letite Passage may give rise to the principal part of their overtides (harmonics) for different reasons.

Tidal constants for Eastport, Me., quoted in Appendix 3 of the Report to the International Joint Commission by the International Passamaquoddy Engineering Board (1959), include $M_2 = 8.65$ $M_4 = 0.20$ $M_6 = 0.15$ indicating a much smaller second and third harmonic content in both tidal height and current at this point than exists within Passamaquoddy Bay.

An attempt to estimate the ratio of the transports in the two passages by relating the amount of a harmonic component in the two passages to the resultant harmonic observed in the rate of change of tidal height in the bay proved unsuccessful.

CALIBRATION OF INSTALLATIONS

Since the constant K of Equation (2) may differ in the two passages, direct measurements of the current were necessary to obtain a calibration.

Current measurements taken at eight locations (Fig. 7 and 8) in the passages proved useful in effecting calibrations. Because of the strong tidal currents in the passages (up to 10 ft/sec) at constriction points, it was felt that the best calibration could be accomplished by making measurements at the inner end of the passages where the cross-sectional areas are greater, and hence the currents reduced. Six locations (Sta. 23, 24, 25, 26, 27 and 28) were occupied for 13- or 25-hr periods (Fig. 7 and 8). Very marked differences were indicated from station to station in each passage (Forrester, 1960), and hence only rough approximations could be made for total flow of water throughout the entire section. Two other anchor stations (51 and 53), located near the constriction points in Letite and Western Passages, combined with Sta. 26 in Little Letite Passage, proved useful for calibration purposes (Fig. 7 and 8).

From available charts together with echo-sounding data, the minimum cross-sectional area in each passage, for each hour of the tidal cycle, was determined (Table IV). In Letite Passage this section passed through Sta. 51. In Western Passage Sta. 53 lay very near to the minimum cross-section, while in Little Letite Passage the location of the minimum cross-sectional area varied with the phase of the tide. The mean minimum cross-sectional areas for Western, Letite and Little Letite (including Doyle) Passages were found to be respectively 61, 34 and 5% of the total.

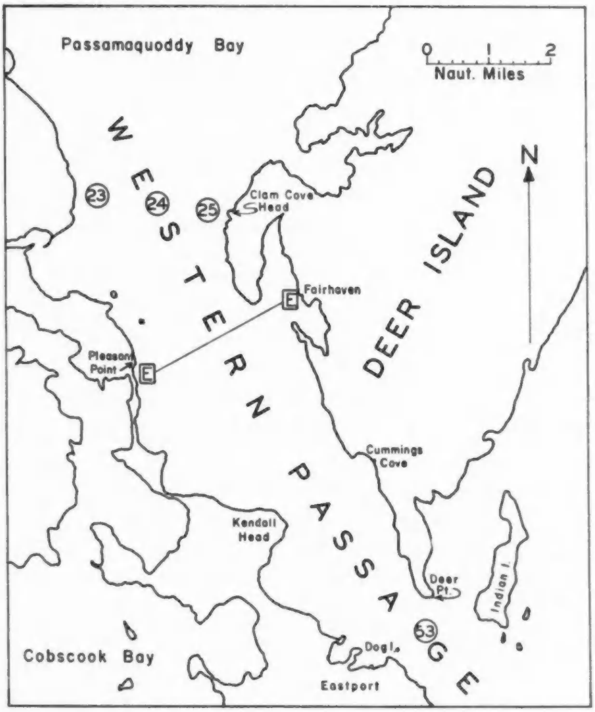

Passamaquoddy Bay
0 1 2
Naut. Miles
N
WESTERN PASSAGE
DEER ISLAND
23
24
25
Clam Cove Head
Fairhaven
E
Pleasant Point
E
Cummings Cove
Kendall Head
Deer Pt.
Indian I.
53
Dog I.
Eastport
Cobscook Bay

FIG. 7. Western Passage showing location of installation and current measurement stations.

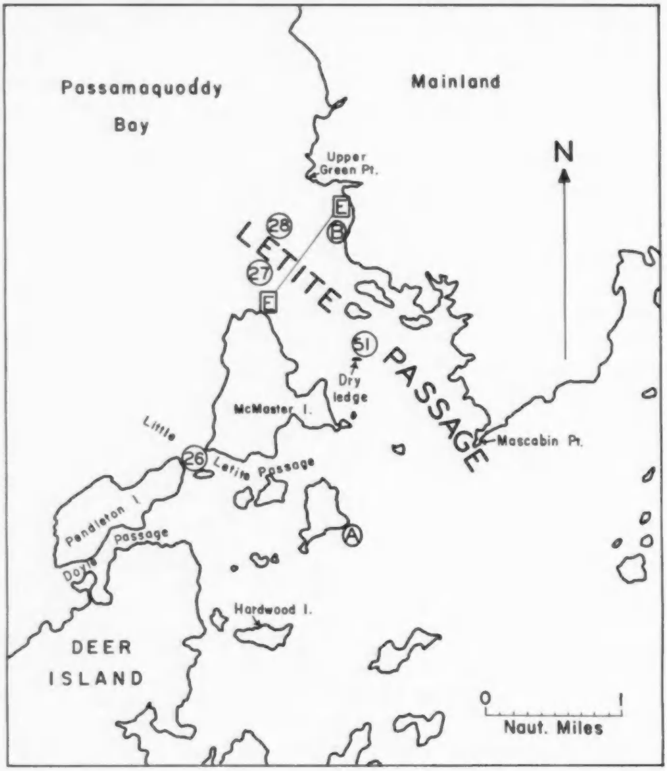

Passamaquoddy Bay
Mainland
Upper Green Pt.
N
E
B
28
27
LETITE PASSAGE
E
51
Dry ledge
McMaster I.
Little Letite Passage
26
Mascabin Pt.
Pendleton I.
Doyle passage
A
Hardwood I.
DEER ISLAND
0
1
Naut. Miles

FIG. 8. Letite Passage showing location of installation and current measurement stations.

TABLE IV. Minimum cross-sectional areas in passages for each hour of tide.

Section		High water	HW+1	HW+2	HW+3	HW+4	HW+5	HW+6	Mean
Western Passage	(ft² × 10⁵)	3.58	3.49	3.38	3.28	3.18	3.08	2.98	3.28
	(% of total)	57	58	59	60	62	63	65	61
Letite Passage	(ft² × 10⁵)	2.17	2.06	1.95	1.84	1.73	1.62	1.51	1.84
	(% of total)	35	34	34	34	33	33	33	34
Little Letite and Doyle Passages	(ft² × 10⁵)	0.53	0.46	0.38	0.32	0.25	0.18	0.11	0.32
	(% of total)	8	8	7	6	5	4	2	5
Total	(ft² × 10⁵)	6.28	6.01	5.71	5.44	5.16	4.88	4.60	5.44
	Percentage	100	100	100	100	100	100	100	100

By using the ratio of the cross-sectional area at a current-measurement station to the minimum cross-sectional area, the velocities at the constriction points were found to be nearly equal for the three passages. It was concluded therefore that the volume of water flowing through each passage was proportional to the minimum cross-sectional area. Using these proportionality values, together with the intertidal volume of Passamaquoddy Bay, the constant K was determined as 1.3 for the Letite installation and 1.4 for the Western Passage installation.

The mean current for the whole cross-section of Letite Passage as obtained from the recorded data using $K = 1.3$, was found to be 80% of the current measured from a ship anchored at Sta. 51, where it was assumed currents close to the maximum value would be found.

The above values of K were applied to the voltage records for a number of different tidal ranges and in all cases volume continuity requirements were acceptably met.

FLOW PATTERN THROUGH THE PASSAGES

The flat-topped features of the Letite voltage record (Fig. 5 (b)) suggested the desirability of further investigation by observing levels on tide staffs at the ends of Letite Passage.

A similar flat-topped transport curve was observed in voltage measurements of the flow through First Narrows which is located at the entrance to Vancouver Harbour, B.C., (G. L. Pickard, personal communication). Direct measurements of the current, carried out independently by W. D. Baines (then at University of British Columbia), also revealed the same feature. It was concluded from this study that the flat-topped characteristic is a consequence of frictional control of the flow.

In Letite Passage simultaneous readings of tidal height for a 13-hr period at 10-min intervals were taken at positions A and B (Fig. 8) while current measurements were read at Sta. 51. The voltage recorders were simultaneously in operation at Letite and Western Passages. Plots of these data are shown in Fig. 9.

No levelling was carried out between A and B. It was assumed that the mean level over a 12.4-hr period was the same at these stations (Fig. 8). Curve C (Fig. 9) is the head between the two points computed on this basis. Curve D is the tidal height at St. Andrews, E the velocity at Sta. 51, F the electrode voltage recorded across Letite Passage, and G the electrode voltage recorded simultaneously across Western Passage. In Fig. 9 the following features are noted:

1. The tidal range inside Passamaquoddy Bay at Sta. B exceeds the tidal range at Sta. A (outside) by 1.2 ft. High water and low water occur respectively 10 and 16 min later at Sta. B inside than at Sta. A outside.

2. Slack water at Sta. 51 corresponds closely with high and low water at Sta. A.

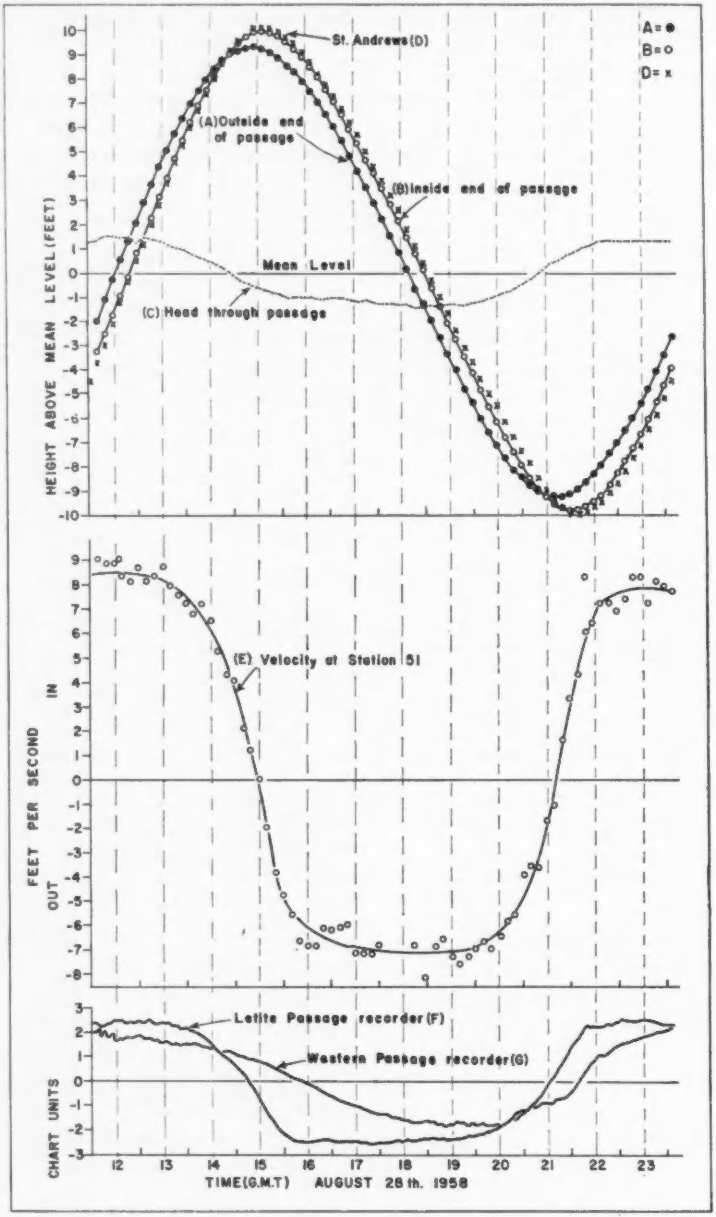


FIG. 9. Graphs of tidal heights, head and velocity for Letite Passage, and voltage records for Letite and Western Passages.

3. The tidal amplitude curve for St. Andrews corresponds closely both in phase and range to that for Sta. B.

4. The voltage records indicate that slack water in Western Passage occurs 35 minutes later than in Letite Passage.

5. Maximum head between the ends of Letite Passage (Sta. A and B) is 1.5 ft on the flooding tide and 1.4 ft on the ebbing tide.

6. The curve for the current at Letite as measured by the voltage recorder and the curve for the current measured at Sta. 51 correspond closely in form.

7. A graph of the square root of the level difference of points A and B in Letite Passage agrees closely in form with the flat-topped current curve of the Letite installation. Thus the current in this passage is one of hydraulic flow, or frictional tidal flow as Pillsbury (1939) has preferred to term it, with the flow determined by the square root of the head and in phase with it.

8. The level inside Passamaquoddy Bay continues to rise normally for approximately a quarter hour after the tidal stream reverses in Letite Passage and a fairly high outward flow has developed there. This rise is to be accounted for by the continuing inward flow in Western Passage which persists for a half hour after slack water in Letite Passage. This is clearly indicated by the voltage records of the passages (curves F and G).

Western Passage, with a greater cross-sectional area and more regular channel than Letite Passage, controls in large measure the level of water in Passamaquoddy Bay. If the tidal wave in the Bay of Fundy is propagated into Passamaquoddy Bay principally through Western Passage without undergoing major changes owing to frictional and topographical effects, an increased tidal range relative to that seaward of the passages is to be expected within Passamaquoddy Bay since it is more distant from the source of the driving tidal oscillation.

RESIDUAL FLOW

As the flow in Little Letite Passage and Doyle Passage is a small part of the whole exchange, it is assumed that the residual flow in these minor passages is not significant. Examination of the transport in the two larger passages (Fig. 10) shows, usually, an outward residual transport in both passages, averaging 10% of the Passamaquoddy Bay tidal prism for Western Passage and 3% for Letite Passage. As the ebb and flood transport must balance except for the run-off into Passamaquoddy Bay, which is considerably less than 1% of the tidal prism, it is clear these data are inconsistent.

From these data it is concluded that there is a small residual outward transport in Western Passage, less than 7% of the tidal prism for Passamaquoddy Bay, and a compensating inward transport in Letite Passage less than the former by the run-off to Passamaquoddy Bay. This tentative inference must await confirmation by additional data.

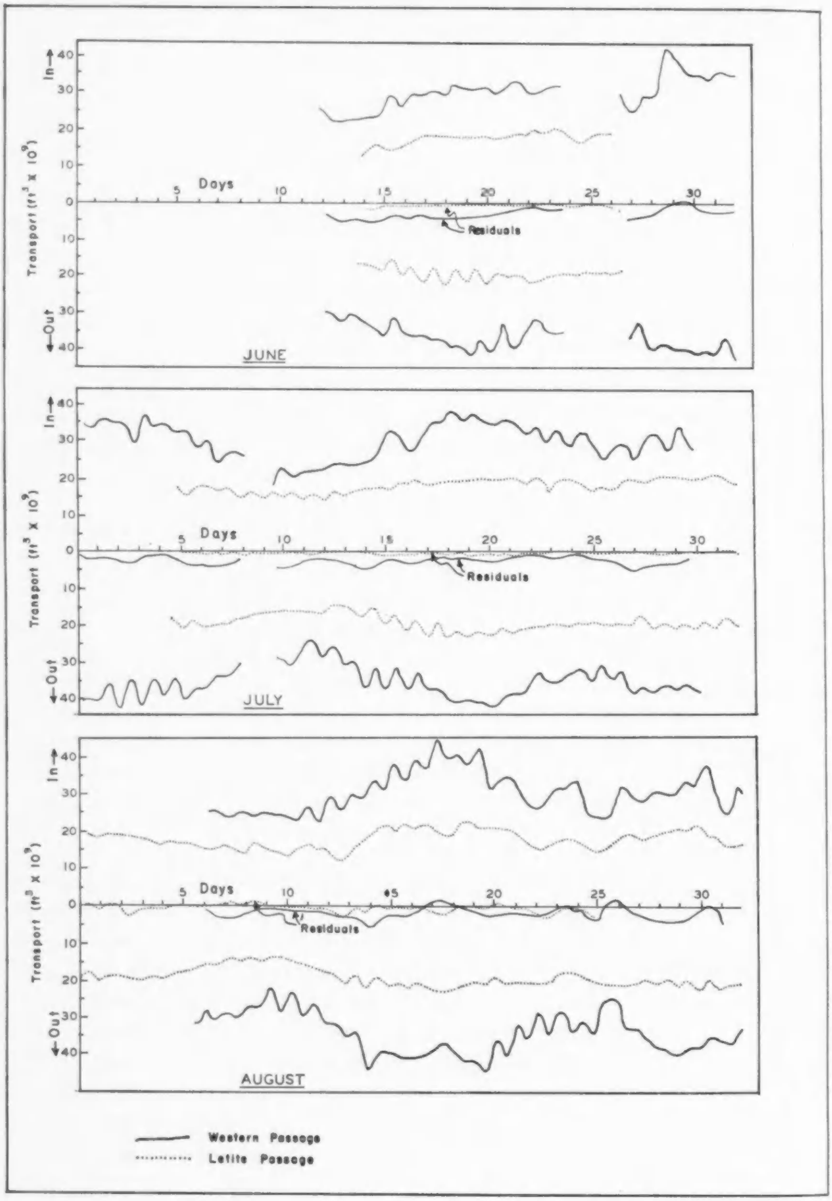


FIG. 10. Transport in Western and Letite Passages for ebb and flood tidal streams, June-August, 1958.

EARTH CURRENTS AND MAGNETIC STORMS

At times the recorder charts showed peculiar features. During thunder storms, lightning strokes were recorded as transverse lines of extremely short duration without any continuing effect on the pen position. Frequently these "lines" would predominate on one side of the mean signal during the early part of a storm and gradually shift to the other side of the trace as the storm progressed (Fig. 11).

Irregularities of the sort reported by Wertheim (1954), Bowden (1956) and others, were observed to occur from time to time. These "storms" developed with sudden displacements of increasing amplitude and reversals extending sometimes to the full extent of the chart paper. These may be best appreciated from Fig. 11 which shows a typically "quiet" record, one disturbed by lightning, and a typical disturbance due to other causes which are presumably associated

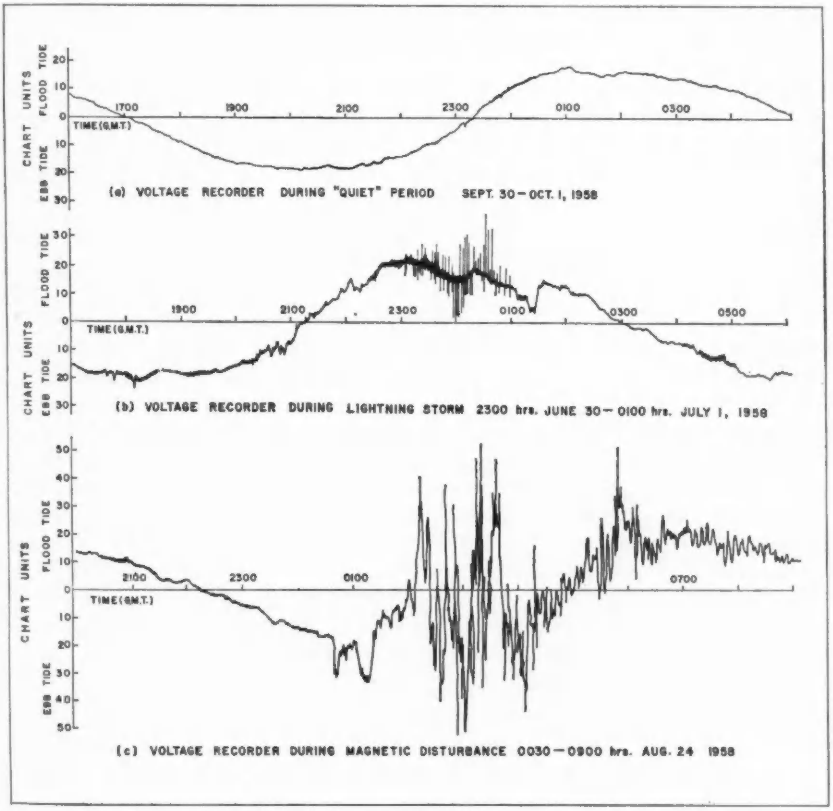


FIG. 11. Typical voltage records for (a) quiet period, (b) lightning storm, and (c) magnetic disturbance.

with earth currents of geomagnetic and/or ionospheric origin. In several instances aurora displays were noted to occur at the same time as the latter type of voltage disturbance. The records from Western Passage showed these irregularities to a much greater degree than those of the installation at Letite Passage. Only for a brief period during the worst of a "storm" as recorded in Western Passage would there be any irregularity shown in the Letite record.

Summaries of the *K*-indices of geomagnetic activity for 3-hr intervals at Agincourt, Ont., were provided by the Dominion Observatory. The index runs from 0 for no fluctuation, to 9 for a fluctuation of 600 gammas. The maximum possible daily total is thus 72. The half-daily totals are plotted in Fig. 12, which also shows periods when large disturbances were recorded at an electrode installation. It can be readily seen that for an unusually high half-daily total (15 or greater) there is a corresponding disturbance produced on the recorder. Although the summaries of geomagnetic activity do not permit a precise comparison of the times of onset of a disturbance, it appeared that the two events occurred nearly simultaneously and in all instances were definitely less than 3 hr apart.

Electrochemical Errors of Electrodes

If the electrodes are placed in water of differing temperature and/or salinity, a voltage will be developed proportional to these differences. von Arx (1950) made a study of this and calculated the theoretical Temperature Coefficient of Potential for the range 0–30°C to be –0.00059 volt /°C. The theoretical Salinity Coefficient of Potential was calculated for a range of 26–36‰ of NaCl solution and found to have a value of –0.00069 volt /‰. Both of these values have been found to be in satisfactory agreement with laboratory experiments.

The possibility of extraneous voltages arising from these differences was considered for each electrode site. For the St. Croix installation temperatures and salinities were observed at low water and high water at the electrode locations. For the other installations, conclusions were drawn as to probable variation from the numerous temperature and salinity observations taken in the Passamaquoddy area during 1957 and 1958 (Forgeron, 1958, A.O.G. 1959). Variations in temperature between high water and low water ranged from near zero in the area seaward of the passages to approximately 0.5°C and 0.5‰ respectively, near the Biological Station. In general the differences in temperature and salinity between one electrode pair was of similar magnitude to the changes tidally at each electrode. Generally, between April and October there is an inverse correlation between salinity and temperature changes tidally. Hence the temperature and salinity differences affect the signal in opposite senses.

Vertical variations in properties are small owing to the vigorous mixing created by strong tidal currents in the area under investigation (Forrester 1960). Although electrode pairs were placed at unequal depths the voltages arising from temperature and salinity differences with depth were considered negligible.

The maximum error introduced in Eqn. (2) owing to temperature and salinity differences was considered to be less than 2% of the maximum signal in all cases. No attempt was made to effect this correction to the records.

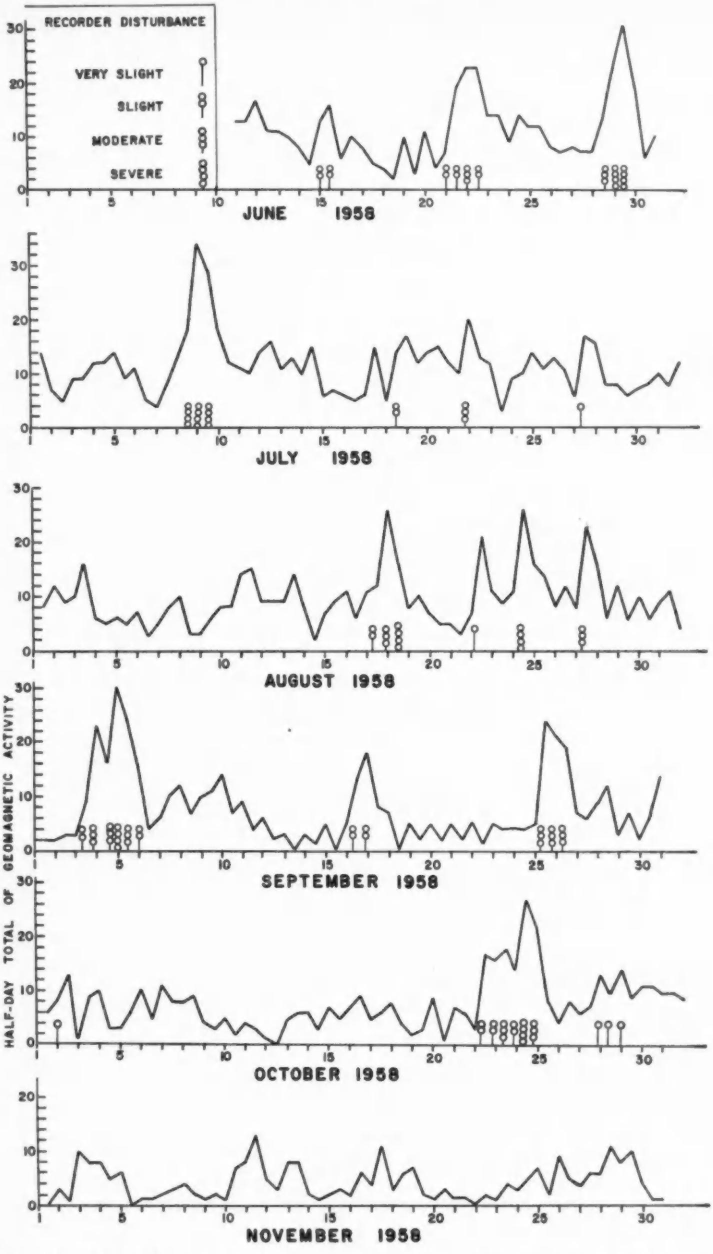


FIG. 12. Half-daily totals of geomagnetic activity index, Agincourt, Ont., and associated disturbances of recorder, June–November, 1958.

SUMMARY AND CONCLUSIONS

The electromagnetic induction method has been applied to measure water transports in the Passamaquoddy region, and the following conclusions have been drawn from these studies.

1. Western Passage supplies about 61% of the water entering Passamaquoddy Bay, Letite Passage about 34%, and 5% is supplied through Little Letite Passage and Doyle Passage.

2. The constant K of equation (2) was computed for the St. Croix estuary, Letite Passage, and Western Passage, and found to be 1.2, 1.3, and 1.4 respectively.

3. During the period of observation, it is concluded that the residual flow in the passages, although not large, was predominately out of Western Passage, and thus inward through Letite Passage.

4. The harmonic analysis of the voltage records for Letite and Western Passages indicates the presence in appreciable proportions of second and third harmonic components. It is inferred that the high third harmonic content in the Letite record is due to hydraulic flow proportional to the square root of the head, while the second harmonic content particularly evident in Western Passage is the result of shallow-water wave distortion.

5. Disturbances presumed to be brought about by earth currents were frequently observed at the Western Passage installation and in the St. Croix estuary, and normally occurred when the geomagnetic activity index at Agincourt, Ont., exceeded 4. The Letite records were disturbed only when the geomagnetic activity index exceeded 8.

6. The average duration of the flooding tide into Passamaquoddy Bay is approximately 6.0 hr, while the tide ebbs for an average period of 6.4 hr.

7. Times of slack water in Western Passage occur later than in Letite Passage. This phase lag varies from about 15 to 60 min. No explanation of this variation was found.

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The authors wish to express their sincere appreciation to the Canadian Hydrographic Service whose team, under the supervision of Mr W. D. Forrester, co-operated in carrying out various aspects of the field work involved in this project; to the New Brunswick Telephone Co. for the use of its cable at Lubec, Me.; and to the Dominion Observatory for magnetic data.

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Annual Cyclic Changes in the Physical Oceanography of a British Columbia Fjord[1]

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ABSTRACT

Indian Arm (49°30′N, 122°53′W), one of the characteristic fjords of the coast of British Columbia, was intensively studied during 35 approximately monthly cruises during 1956 through 1959, with the main objective of determining the annual cycle of its oceanographic features. Unique in its duration of a British Columbia fjord study, this observational time series of the distributional patterns of salinity, temperature, density, dissolved oxygen and climate is presented, and used to analyze the circulation pattern and replenishment mechanism of fjord waters.

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1. INTRODUCTION

On certain high-latitude coastal sections of the northern and southern hemispheres, there are characteristically long, narrow, deep arms of the sea referred to as fjords. Although these fjords are restricted to a small percentage of the total coast line in these latitudes, their unique characteristics and local importance have brought them particular attention. They are usually associated with four regions: the west coast of North America from British Columbia north

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into Alaska, the west coasts of Norway, Chile, and New Zealand's South Island. In addition they are common along the coasts of Newfoundland, Labrador, Baffin Island, Greenland, Iceland, Scotland, Spitzbergen, Novaya Zemlya, and the Kerguelen Islands.

Although it is not possible to establish a strict definition that applies in all instances, a combination of geological features distinguishes fjords from other types of narrow embayments. A fjord usually exhibits most of the following features: it is located on a glaciated coast which has undergone post-glacial isostatic uplift; it is a basin, usually over 100 m deep, partially separated from the adjoining sea by a threshold or sill; it is a long narrow waterway with roughly parallel sides or an interconnected system of such waterways; it is U-shaped in profile with steep valley walls.

In the North Pacific "...between the forty-ninth and fifty-ninth parallels the mountainous western margin of North America meets the Pacific Ocean in a deeply indented, island-studded coast ranking with the grandest fjord-coasts of the world in the character and magnitude of its physical features" (Peacock, 1935). Occupying two-thirds of this region is the British Columbia coast, on which are located some forty fjords not including those located on Vancouver Island and the Queen Charlotte Islands. One of these mainland fjords, Indian Arm, some 10 miles northeast of Vancouver, B.C. (Fig. 1), was selected for this study. It connects with Burrard Inlet, the lower portion of which forms the harbour of Vancouver.

Prior to about 1930 fjord oceanography in British Columbia was virtually unstudied. Even today many of the fjords remain incompletely sounded and charted. Since 1948 several research projects have provided much information on the physical oceanography of the fjords, although the field investigations of most of these were restricted to summer months.

Much of the oceanographic research on British Columbia fjords (Hutchinson, 1929; Carter, 1932, 1934; Tully, 1936, 1949; Pickard, 1955; Trites, 1955; Tabata and Pickard, 1957; Giovando, 1959; Pickard, 1961) has dealt with the distribution of conservative oceanographic properties. The bulk of this research has been conducted during the summer months and little has been known of the seasonal distribution of these properties. Tabata and Pickard (1957) worked with data gathered on 11 cruises during a 2-year period, with gaps between successive cruises ranging up to 5 months. During 1931, the Biological Board of Canada (now the Fisheries Research Board of Canada) made limited observations on 9 cruises over a period of one year in Indian Arm. With these exceptions, all previous work has been conducted primarily during the summer months. Since 1951 until the work described in this paper, only 3 of the 19 other cruises conducted in British Columbia fjords were made between October and May. This work is based upon data collected on 35 cruises at approximately monthly intervals over a period of slightly over three years, and is the most complete set of oceanographic data available on a British Columbia fjord. It provides a unique opportunity to establish in some detail the characteristic annual cycle of fjord oceanographic properties.

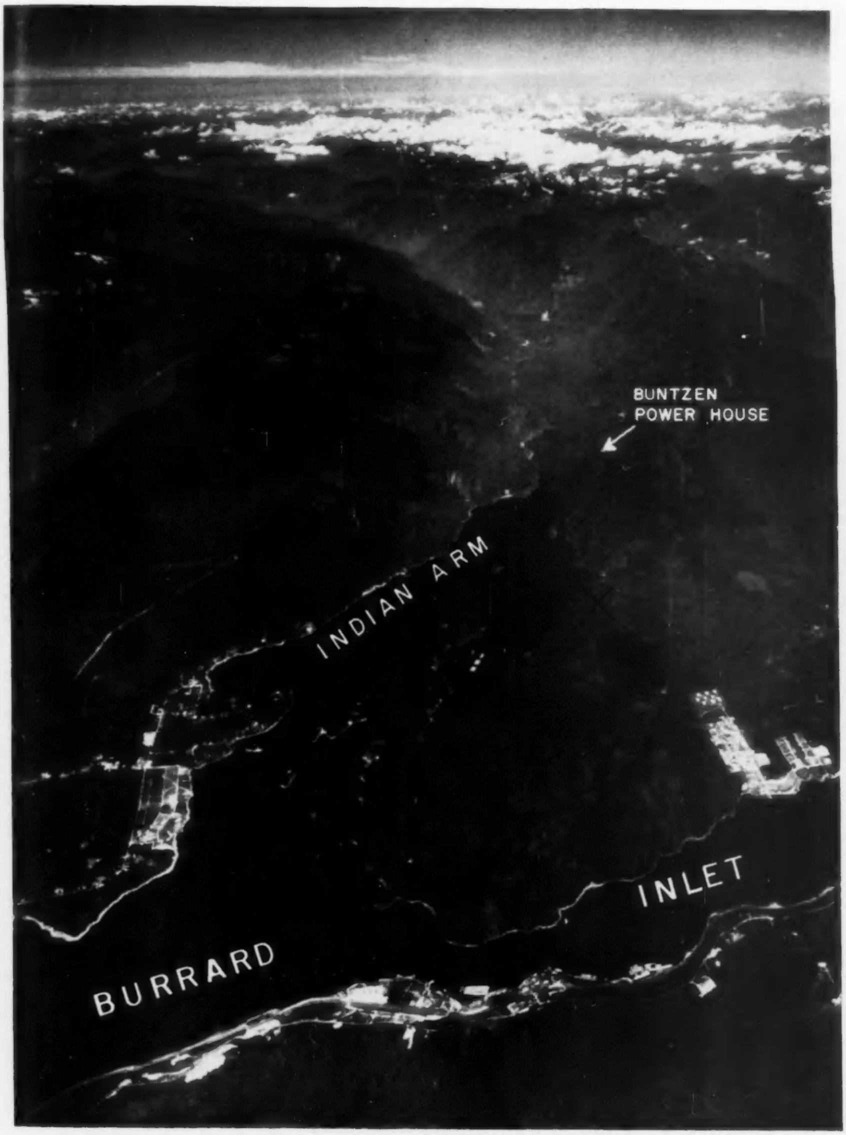
BUNTZEN
POWER HOUSE
INDIAN ARM
INLET
BURRARD

FIG. 1. Oblique aerial view looking north into Indian Arm. (B.C. Government Air Photo.)

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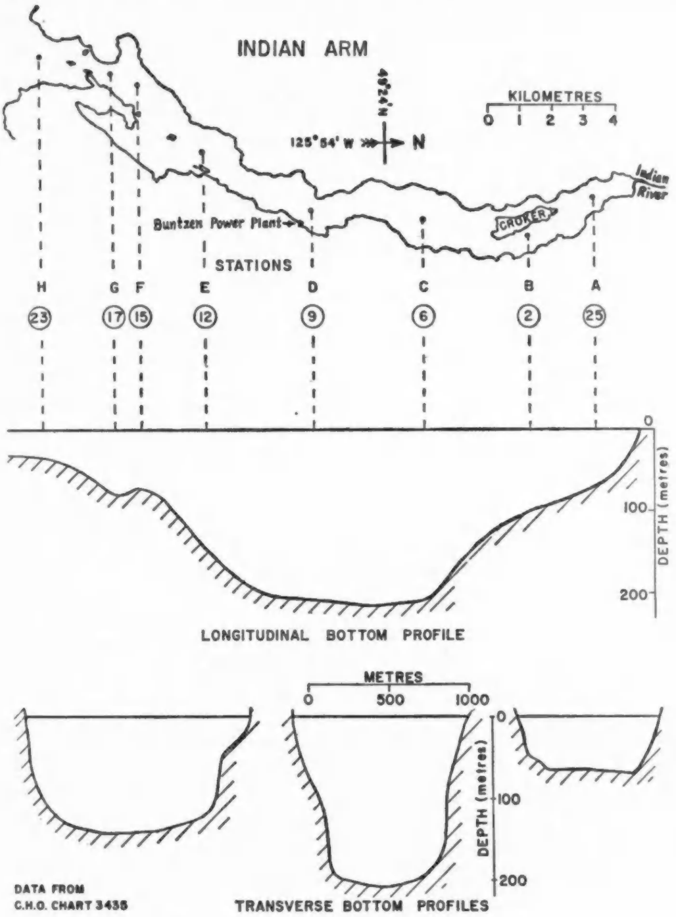
2. PHYSICAL FEATURES

2.1. Physiography and Geology

Indian Arm extends almost due north into the coast range from a point at Lat. 49°18′10″N, Long. 122°56′20″W, thus placing it near the southern end of the British Columbia fjord system. An aerial view (Fig. 1) shows a typical fjord appearance — a long, narrow embayment bounded by a precipitous mountain wall. The total length of Indian Arm is 22.1 km and its average width is 1.3 km, yielding a length–width ratio of 17:1. The major portion of the inlet is characterized by a deep basin with an average depth of 200 m and a maximum depth of 245 m. Figure 2 shows station positions in Indian Arm and


INDIAN ARM
49°24′N
125°54′ W
N
KILOMETRES
0 1 2 3 4
Indian River
CROKER
Buntzen Power Plant
STATIONS
H G F E D C B A
㉓ ⑰ ⑮ ⑫ ⑨ ⑥ ② ㉕
0
100
200
DEPTH (metres)
LONGITUDINAL BOTTOM PROFILE
METRES
0 500 1000
0
100
200
DEPTH (metres)
TRANSVERSE BOTTOM PROFILES

DATA FROM C.H.O. CHART 3435

FIG. 2. Plan of Indian Arm showing station positions, longitudinal, and transverse bottom profiles.

longitudinal and transverse bottom profiles. Indian Arm follows a somewhat sinuous course from the mud delta of the Indian River, which marks the northern-most end of the fjord, to the wide, shallow sill at the mouth where it connects with Burrard Inlet. Two features deserve particular comment: the maximum depth of 26 m at the sill, and the constriction which exists about 2 km north of the mouth of the fjord. As will subsequently be discussed, these features play an important role in the dynamic oceanography of this fjord.

The formation of the British Columbia fjord system has been investigated in some detail (Bancroft, 1913; Carter, 1934; Peacock, 1935) with the conclusion that both tectonic movements and glacial action have been instrumental in the formation of the present system. Tectonic forces and movements produced a fractured and deeply dissected plateau before the beginning of the latest glacial epoch. A combination of longitudinal and horizontal fault patterns guided the erosive action forming an immature valley system which was subsequently subjected to glacial excavation during the descent of glaciers from the major ice sheets. The thickness of the glaciers prevented their floating when they reached sea level and thus their scouring action extended well below sea level. The characteristic fjord structure subsequently resulted from a combination of local subsidence and glacial retreat, and the glacial-scoured, drowned-valley system formed two patterns of fjords in British Columbia, running primarily NE–SW and NW–SE.

The basic fjord pattern of two systems intersecting at 90° divides the majority of fjords into two divisions. Most of the mainland fjords, which are of the first division, lie transversely to the mainland coastline. These fjords normally receive the drainage of a river at the eastern end and are open to the sea at the western end. Those of the second division tend to lie parallel to the coastline and often are smaller in size. These may connect two or more of the mainland fjords.

The first division, represented by 33 fjords in British Columbia, is considered to be the most typical of this coast. General physiographic features are similar within this division. They range in length from 6.5 to 114 km and in average width from 0.6 to 6.0 km. The width of fjords appears to be correlated with length. With only, four exceptions, the ratio of fjord length to width is between 12:1 and 50:1. The average ratio is 20:1. The mid-inlet depth of the fjords ranges from 76 to 510 m, with an average depth of 270 m; the maximum depth ranges between 100 and 730 m, with an average maximum depth of 388 m. The depth of the sill is between 6 and 363 m, more than 50% being less than 75 m. The greatest physiographic differences between fjords are found in the wide variations of sill depths at the entrance and in the presence or absence of inner sills.

Physiographic features and dimensions of Indian Arm place it within the main division of British Columbia fjords. Its length and width are slightly less than average. It differs in having a shallower sill than most British Columbia fjords. The 26-m deep sill is appreciably shallower than the average sill depth of 106 m found in other fjords, yet it is not the shallowest sill in the

British Columbia fjords. Therefore, with the possible exception of the sill depth, Indian Arm can be considered physiographically typical of British Columbia fjords.

2.2 BOTTOM SEDIMENTS

The characteristics of the bottom sediments of Indian Arm are shown in Fig. 3. This analysis is based upon 18 samples collected with a Dietz–LaFond snapper along 6 cross-fjord transects. On each transect samples were collected from both eastern and western flanks and from the center of the fjord. All samples were light grey in colour, indicating non-stagnant conditions (Twenhofel,

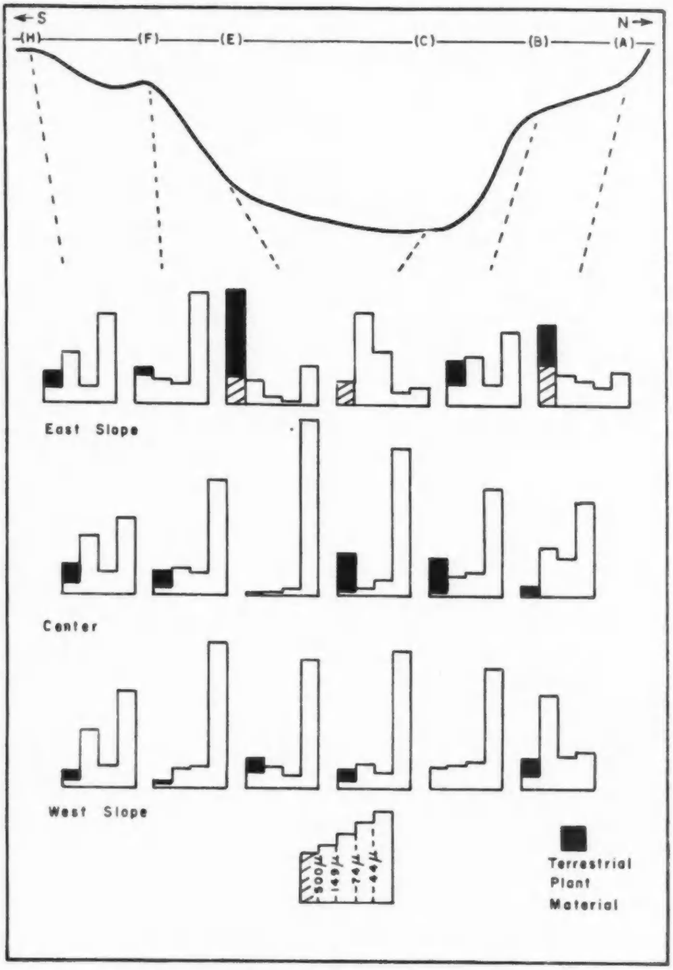


Fig. 3. Longitudinal distribution of bottom sediments.

1939). With a few exceptions, samples contained very little organic material. The predominant organic material consisted of leaves from deciduous trees, pine needles, small twigs and wood chips. No appreciable H_2S odour or varves were noted in any of the samples.

The particle composition of the samples collected along the deep center line of Indian Arm shows certain consistent trends. The relative proportion of clay particles increases with distance from Sta. A toward Sta. D. The slight departure from this trend shown by the presence of clay in the sample from Sta. B may be attributed to the increased current velocities at this station. This would result from the small cross-sectional area of the channel adjacent to Croker Island. Conversely, the proportion of silt decreases with distance from Sta. A toward Sta. E, and the proportion of sand also decreases but at a much faster rate. It is believed that progressive sorting has occurred with distance from the head of the fjord. Heavier particles are deposited closer to their original source. This is consistent with that reported for the distribution of sediments in Bute Inlet (Toombs, 1956).

Samples collected at three widely separated points across the mouth of the fjord (Sta. H) show a similar distinctive pattern of particle size distribution, even though they were collected at different depths. This strongly suggests that the same current pattern and water mass are present at all points across the mouth of the fjord. In addition to being consistent, the distribution pattern here is quite different from that observed within the fjord. The high proportion of sand is particularly noticeable. This difference suggests that much of the water in this region has an immediate origin different from that of the water from within the fjord. When the distribution pattern of the stations just inside the "narrows" (the lateral restriction between Sta. G and H) is examined, another point is apparent. The distribution of particle sizes found in the center sample of Sta. F is intermediate between that found at the mouth of the fjord at Sta. H and that found within the fjord at Sta. E, indicating that there has been intrusion of the outside waters and progressive sorting of the suspended particles.

Except in two sets of samples, the different depths of the east and west flank samples preclude comparison. However, two sets do show cross-fjord differences, as, for example, in the east and west set collected at Sta. F, which is just inside the narrows north of the sill. The west flank sample contains a relatively higher proportion of clay than the east flank sample, and conversely, the east flank sample contains a relatively higher proportion of sand and silt. If it is assumed that the waters entering the fjord from Burrard Inlet contain a higher proportion of large-sized particles than contained in corresponding waters within the fjord, an assumption that is consistent with the water's history of tidal passage through a region of extreme turbulence at the second narrows of Burrard Inlet, this would indicate that waters entering the fjord tend toward the eastern side of the channel. Such a current distribution would result in the deposition of a higher proportion of larger particles toward the eastern side and the deposition of a higher proportion of clay-size particles along the western side of the channel. This type of estuarian current pattern results from the effects of Coriolis force (Pritchard, 1952).

The sediment samples taken across the fjord at Sta. A show an increase in the proportion of sand from east to west. This can be attributed to the Indian River, which enters at a point toward the western side of the head of the fjord.

In summary, the bottom sediments of Indian Arm suggest that:

a. Progressive sorting occurs along the fjord length in two directions, both north and south, indicating two primary sources of suspended material: namely, the Indian River and intruding outside waters from Burrard Inlet.

b. Waters entering the fjord tend to flow inward along the eastern side of the channel, and outward toward Burrard Inlet along the western side of the channel.

c. Non-stagnant conditions prevail.

3. DISTRIBUTION OF CONSERVATIVE OCEANOGRAPHIC PROPERTIES

3.1. SALINITY

Two features control the salinity distribution in Indian Arm: the connection with adjoining basins, and the fresh water entering the fjord. The former results in the bulk of fjord water being saline. The latter subsequently reduces the salinity of this saline water. Therefore the fjord is a positive estuary, since it contains sea water measurably diluted with fresh water (Pritchard, 1952).

The fjord's water mass tends to exist as a two-layer system because of the quantity of fresh water which flows into the fjord. A thin layer of brackish water at the surface overlies a more saline water mass. The principal variations in time and space which occur within the fjord are differences in thickness of this brackish water layer and differences in the surface salinity gradient from the head to the mouth of the fjord.

The annual changes in the salinity distribution of Indian Arm are clearly discernible and consistent. The same basic pattern was observed during each of the three years of this investigation. Figure 4 presents this repeating pattern for nine depths of a single station representative of the fjord water mass. The annual changes can be divided into four periods, each of which approximately corresponds to the variations in the seasonal input of fresh water. These four periods are: the late winter minimum from January to March, the spring maximum from April to June, the mid-summer minimum from July to September, and the early winter maximum from October to December. For convenience, the longitudinal and vertical salinity gradients will be discussed in detail for the period of highest runoff (the spring maximum), followed by a discussion of the seasonal deviations from this basic pattern. Finally, long-term deviations from the basic annual cycle will be discussed.

The time of highest runoff of the spring maximum varied from year to year. These maxima occurred during May in two years and during June in one year. It should be noted that two factors suggest these means may not include the lowest values present in the fjord during the year. It is known that the fresh water discharge may fluctuate over 100% within a few days (*Anon.*, 1956c, 1957c, 1958c, 1959c). These fluctuations, combined with the fixed monthly scheduling of the oceanographic cruises, make it impossible to be certain that the observations were always made precisely at the time of maximum fresh water discharge. Although the mixing and seaward movement of the fresh water tend to smooth these short-term fluctuations, it is likely that surface salinity distribution patterns fresher than those presented in Fig. 4 occurred during the spring maximum.

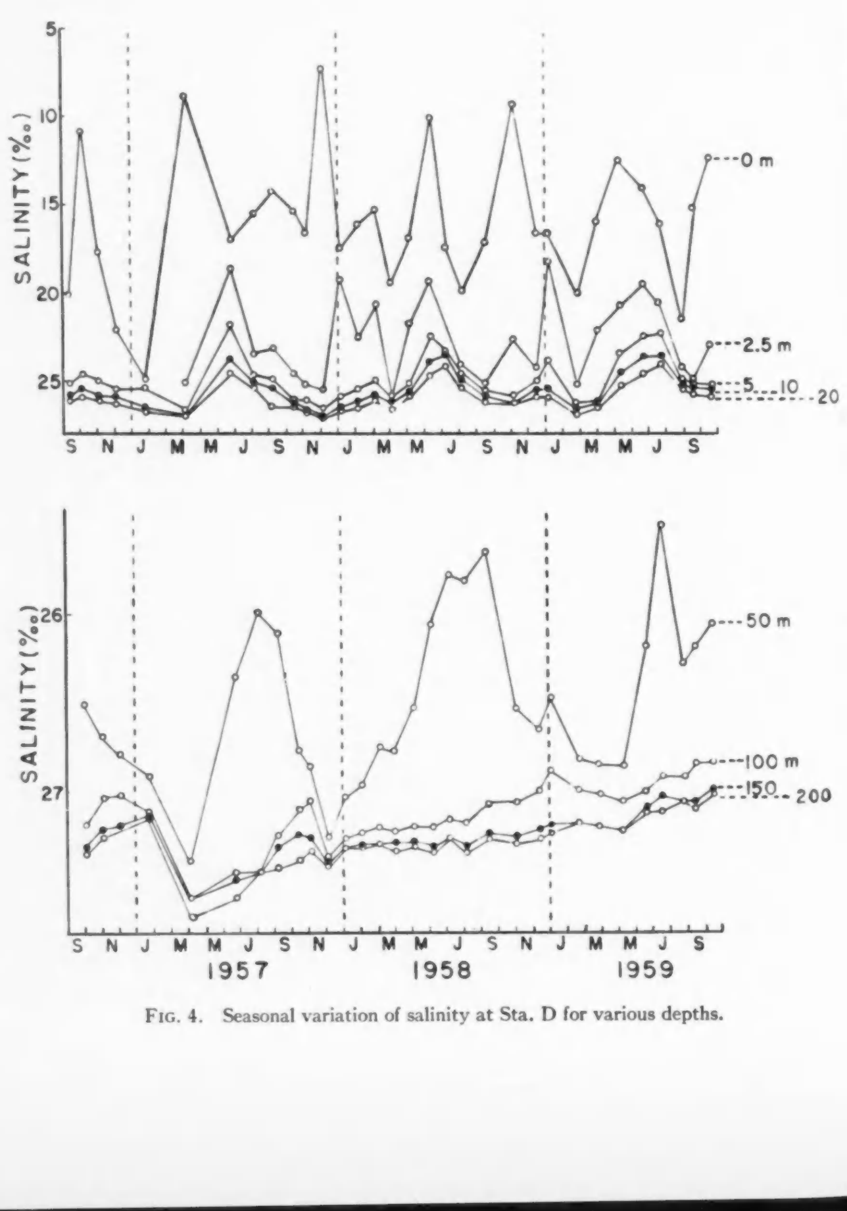


FIG. 4. Seasonal variation of salinity at Sta. D for various depths.

The seaward salinity gradient previously reported for British Columbia fjords (Pickard, 1955) is present in Indian Arm. During the three years of this investigation, at the time of spring maximum runoff, salinities were 0.95 to 4.38‰ at the head, increasing seaward to values between 13.16 and 19.40‰ at the mouth. During this spring period, the mean surface salinity change from head to mouth was nearly linear, as shown in Fig. 5.

The greatest departure from a linear relation occurs in the region from Sta. F to Sta. H, and apparently is associated with passage of the surface waters through the "narrows". Here the mean rate of change of surface salinity is 1.10‰ per km, a rate of change over twice the value 0.47‰ observed within the fjord. If the base salinity were considered to be the highest salinity observed in the fjord, these salinities at the mouth would be approximately 60% of base salinity.

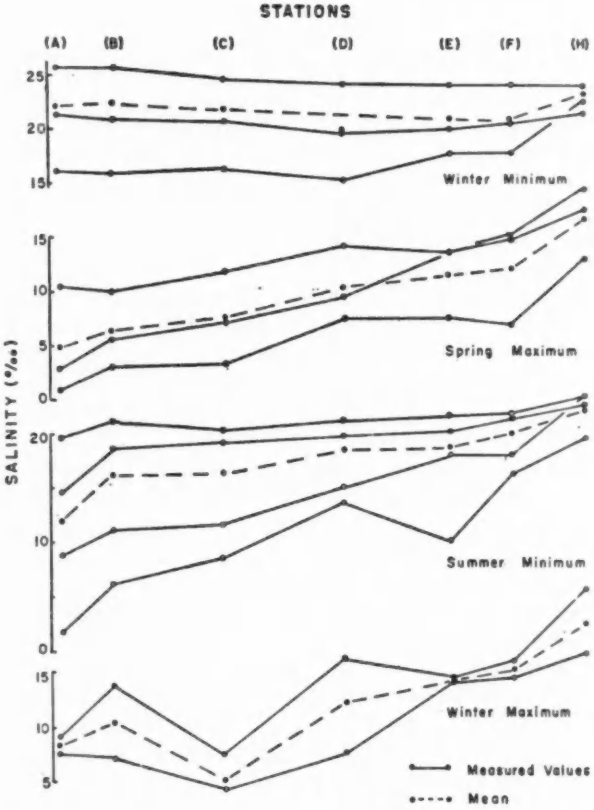


FIG. 5. Longitudinal distribution of surface salinity during 1956 to 1959.

At the head, the vertical salinity distribution exhibits a strongly stratified system composed of an essentially homogeneous layer 1.5 to 2.5 m thick, subtended by a thick bottom layer of much more saline water. These two layers are separated by a transition zone 2.5 to 5 m thick, which has a large vertical salinity gradient. Thus at depths less than 10 m, salinities reach over 90% of base salinity. With distance seaward, as shown in Fig. 6, the deep water retains essentially the same salinity character.

Of the four seasonal salinity distributions, the pattern present during the spring is the most consistent from year to year. This is probably in part due to the nature of the fresh water discharge. During this period, the chief source of fresh water entering via the Indian River and peripheral streams is melt water. Examination of river discharge data shows that discharge during the spring melt period is much more consistent from year to year than the discharge during the fall, when there is direct runoff.

The most clearly defined and most consistent pattern is present during the maximum runoff periods in late spring and early summer. The distribution during this period is shown in Fig. 6. At this time there is a consistent increase in surface salinity, with distance toward the mouth of the inlet. At about 2 m depth, the salinity varies little along the length of the inlet. From about 2 to 18 m, the trend found at the surface is reversed. The salinities decrease with distance toward the fjord mouth. From approximately 20 m to the bottom, the salinities are essentially uniform, except that those in the southern portion of the deep basin are consistently higher than those at corresponding depths in the northern portion of the deep basin. This tendency is strongest during the spring maximum. During other seasons, the mean salinity gradient is small, and the deep water at 75 to 200 m can be considered longitudinally homogeneous.

The mean salinity structure at Sta. H is noteworthy. At this station, located at the sill south of the narrows, there is a much lower mean salinity between 2 and 18 m than at corresponding depths north of the narrows. This pattern can be seen clearly when the mean salinity profile for the spring maximum is compared with the profile for the following summer minimum (Fig. 6). This increase in salinity of surface water, combined with a decrease in salinity at intermediate depths, suggests that intense mixing has occurred when the water moves through the narrows. The higher salinities apparent in the bottom waters suggest that mixing took place down to about 18 m.

Figure 6 shows the mean salinity pattern during the mid-summer minimum, and presents a pattern distinctly different from that present during the spring maximum. During the summer minimum, there is again an increase in surface salinity with distance toward the fjord mouth. The mean salinity increase is from 13 to 22‰. The seaward increase in salinity is apparent down to a depth of 50 m, with constant salinities extending from approximately 75 m to the bottom. This is in contrast to the salinity pattern present during the spring maximum, when constant salinities exist much nearer to the surface at approximately 20 m.

The range of salinities during the winter maximum (Fig. 6) is greater than during the spring maximum. At the winter maximum there is again an increase

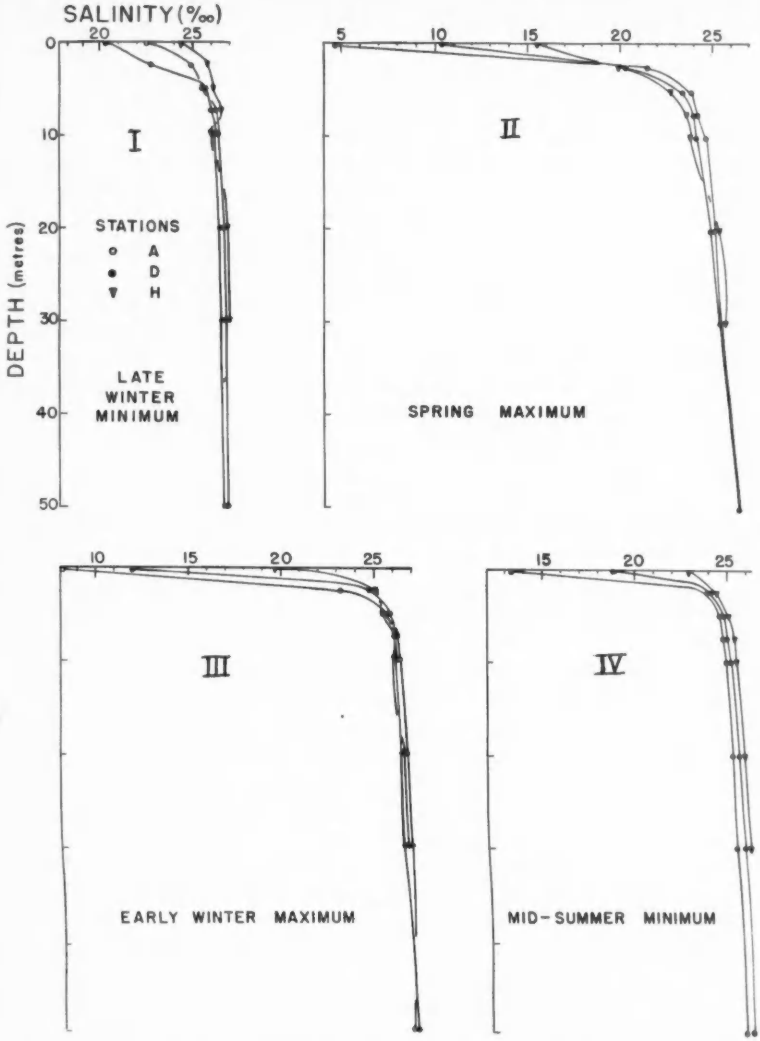


FIG. 6. Mean vertical salinity profile at selected stations during 1956 to 1959: I — Winter runoff minima. II. — Spring runoff maxima. III — Winter runoff maxima. IV — Summer runoff minima.

downstream of surface salinity from 8.2 to 19.8‰. However, the pattern differs in that this longitudinal gradient is present at lower depths than it was in the spring. The water approaches longitudinal homogeneity at about 5 m rather than at 2 m. Below 5 m, the vertical salinity gradient (0.018‰ per meter) is less than one-third that of the spring (0.067‰ per meter). The same apparent effect of mixing at the narrows can be seen in the salinity profile above the sill (Fig. 6). Here the effects of mixing extend to a depth of approximately 12 m, compared with 18 m during the spring. Salinity at 0 to 3 m is greater, and at 4 to 12 m is less, than at corresponding depths north of the sill.

The pattern present during the winter minimum is not nearly as consistent as during the other three periods. In 1956 and 1957 there was a decrease in surface salinity seaward; in 1958, a decrease in salinity to Sta. C and then an increase in salinity to Sta. H. The resulting mean pattern therefore is not considered as representative. This confused picture probably results from the high discharge of fresh water from the Buntzen power plant during low runoff at this time. However, the pattern does not extend to the deeper water masses; here, both longitudinally and vertically the salinity gradients are similar to those found during the other three periods.

Referring again to Fig. 4, the annual salinity distribution discerned in three years is shown for selected depths considered to be representative. Several characteristics are significant. The surface salinity follows very closely the seasonal pattern of runoff, minima occurring both in May and October, and maxima in August and February. However, the salinities at 2.5 m are often significantly out of phase with the surface salinities. This is particularly evident during the last half of the year. Such a characteristic inverse relationship appears to be associated with the mechanism of mixing and tidal feedback at the narrows. From 5 to 50 m the annual cycle is characterized by a single maximum and a single minimum which occur progressively later with increasing depth.

For convenience, the characteristic annual salinity cycle is considered in three zones: 0 to 5 m, 10 to 50 m, and 100 to 200 m.

The surface and inversely related subsurface pattern is controlled by two features: the seasonal discharge of fresh water into the fjord, and the action of the narrows upon the seaward transport of the surface brackish layer. It is hypothesized that the restriction in cross channel width caused by the narrows forces the velocities of tidal currents and the seaward-moving surface layer to increase. If the relative velocity exceeds a critical value, the interface between the surface layer and the next lower layer breaks down and a new, thicker surface layer is formed. This layer continues to move seaward, but at a much lower velocity, which is below the critical value for surface-layer breakdown. During periods of high runoff, the resulting mixed layer still has a salinity low enough that a large density gradient exists between it and the underlying bottom waters. This large density gradient restricts vertical mixing, and as a result the tidal water entering the fjord has a relatively high salinity.

During periods of low runoff, the surface water mixture has an appreciably higher salinity than during high runoff. The density gradient between the surface layer and deep water is then quite small and this, combined with the low velocity of the surface water, results in the tidal inflow extending from the top to the bottom of the water column. Such an inflow, subsequently mixed during passage through the narrows, has a lower salinity than the inflow during periods of high runoff.

The above concept is partially supported by the inverse relation observed in the main fjord basin between the salinities at the surface and subsurface layers. Examination of longitudinal salinity profiles of individual cruises suggests that the thickness of the newly formed surface layer is approximately 18 m during times of high runoff and 12 m during maximum winter runoff. The results of upward mixing can be seen as a marked increase in surface salinity seaward of the narrows, as shown in Fig. 5.

The zone between 10 and 50 m has salinity minima at progressively greater depths as the year advances. The initiation of salinity minima appears to be associated with minima in the subsurface waters during June and July. Its progression downward is probably related to downward mixing of fresher water from this subsurface layer.

In the deepest zone, 100 to 200 m, the distinctive feature is the rather sharp increase in salinity during February and March of some years. Yet even with these annual fluctuations in deep basin waters, the salinity remains quite close to 27.5‰.

When the deep water salinities of all mainland British Columbia fjords are considered, a natural division is evident. Fjords of the northern group have the waters of Hecate Strait and Queen Charlotte Sound as their salt water source; those of the southern group are connected to the Strait of Georgia. As a consequence of the diverse oceanographic characteristics of these bodies of water, the base salinities of the northern and southern groups are significantly different. Those of the northern group average 32.5‰ and of the southern group 30.0‰.

Indian Arm is connected through Burrard Inlet to the Strait of Georgia, and consequently is a member of the southern group of British Columbia fjords; yet its deep water salinities vary significantly from the other fjords of the group. The average deep basin salinity of 27.5‰ varies as much from the average of the southern group as the southern group does from the northern group. This is probably associated with the shallowness of the sill.

Within the southern group there is a further tendency toward separation on the basis of differences in quantity of fresh water discharge. As discussed in the following section on fresh water inflow, the fjords can be divided into high- and low-runoff subgroups. During maximum runoff, the high-runoff fjords have surface salinities approaching 0‰ at the head, and at the mouth have between 70 and 90% of the base salinity for the fjord. In the low-runoff fjords, the salinity gradient from head to mouth is much less. While similar salinities are obtained at the mouth, the salinities at the head may range from 7 to 28‰. Correlated with this horizontal salinity gradient is a vertical gradient which is largest during periods of maximum runoff. At these times, salinities may be as much as 90% of the base salinity at depths of 10 m. During low-runoff periods and in the low-runoff fjords, the salinity gradients are much smaller. The characteristics of Indian Arm agree well with the reported characteristics of the low-runoff group, and it is therefore considered to be a typical member of this group. However, in Indian Arm, in spite of the annual variations in salinity, the total amount of salt contained in the fjord waters is nearly constant. The mean salinity of the water column can be considered an approximate measure of the salt in the fjord. The annual range in this cycle is 0.7‰, and shows a single maximum and minimum. The maximum occurs in March and presumably reflects the annual influx of more saline waters from outside the fjord. The minimum occurs in July and probably reflects the mixing of fresh water.

The most outstanding point in the long-term salinity picture is the existence of a sharp increase in deep water salinity between January and March of 1957 (Fig. 4). Unfortunately, the exact time cannot be established because of a gap in the cruise schedule during this period. At this time, the salinity at all depths from 50 m to the bottom of the fjord increased by nearly 0.5‰, a change in salinity commonly associated with shallower waters. The only source of such comparatively highly saline water is the Strait of Georgia. It is believed that a massive intrusion of relatively highly saline water occurred at this time.

In examining this picture several other points become evident. During November 1957, a similar increase in salinity is apparent at all depths from 50 m to the bottom. During March of 1958 and 1959, the waters from 150 to 200 m were essentially homogeneous, again suggesting an influx during these periods.

The fresh water discharge from the Buntzen hydroelectric power plant, discussed more fully in Section 3.2, has an important bearing on the distribution of salinity in Indian Arm. In order to establish the extent of this influence, a grid of hydrographic stations was occupied near the power plant during October 1957. At this time, the fresh water discharge from the Indian River and from peripheral streams was low and the discharge from the power plant was high. Figure 7 shows the effects of the fresh water influx at 0, 2.5, 5, and 10 m.

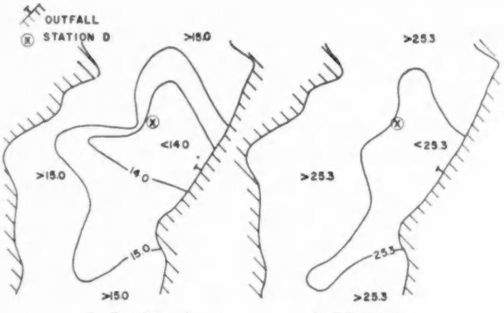
Adjacent to the plant outfall there is a reduction in salinity by about 2.5‰ relative to up-fjord values. Over a wider area, the salinities are reduced by about 1.5‰. At 2.5 m, the affected area is smaller, with an average salinity reduction of about 1.5‰. The intrusion of higher-salinity water from up-fjord is apparent as an indentation in the isohalines opposite the power plant on the west side of the fjord. At 5 m, the fresh water influx lowers the salinity by about 0.2‰. At 10 m, a slight indication is apparent in a salinity reduction of about 0.05‰ in a small water mass immediately opposite the power station.

These data indicate that the effect of fresh water discharge from the power plant significantly reduces the salinity in the immediate area of the plant and primarily influences the surface water along the eastern half of the fjord. The surface water outflow apparently maintains its identity along the western side of the inlet. During periods of low runoff and high discharge from the power plant, the adjacent water mass may have its salinity reduced 2 to 3‰. The influence becomes weaker with increasing depth, and has almost disappeared at 10 m depth.

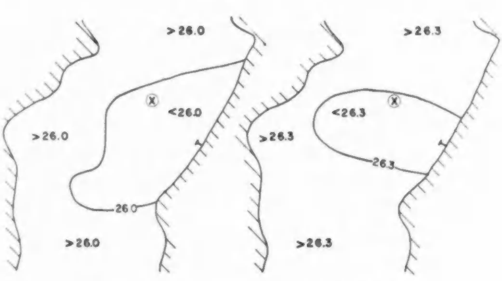
During periods of low discharge, the plant is operated intermittently, at times being closed completely. Such an operation pattern would result in the formation of clouds of fresh water which might retain their identity as they are moved about by tidal currents, wind, and the net seaward motion of the surface brackish water layer. Such clouds could introduce errors in the interpretation of surface salinity measurements; however, the effect would be restricted to the surface water, and would not appreciably influence the deeper water mass.

The surface brackish layer of Indian Arm can be considered as consisting of two zones: an upper zone in which the salinity remains substantially constant from the surface to 2 to 5 m, and a transition zone, the halocline, from 4 to 10 m, where the salinity increases rapidly with depth. Observations relating to the increase in volume and velocity with entrainment of underlying waters led Tully (1949) to suggest that the brackish layer *decreases* in thickness with distance from the head of the fjord, and that a point may be reached where the sharp transition zone becomes blurred. Such a breakdown of the surface layer appears to have been observed by Tully in the course of the oceanographic investigations of Alberni Inlet, a fjord on the west coast of Vancouver Island, but is not strongly supported by the data from Indian Arm. However, it should be noted that the salinity samples are collected in water bottles 50 cm long which would prevent noting a decrease of less than this distance.

The breakdown in the surface layer is assumed to be due to an increase in velocity, attributable to an increase in volume resulting from entrainment. It can be speculated that an analogous situation exists in Indian Arm, but is attributable to a different cause. A reduction in the salinities of the upper 10 m



A. 0 metres B. 2.5 metres



C. 5 metres D. 10 metres

FIG. 7. Influence of the fresh water discharge from the Buntzen power plant on salinity.

can often be seen at Sta. B. This reduction is associated with periods of high runoff and correspondingly high velocity of the surface water. Because of the restriction in channel width in the vicinity of Croker Island, the critical velocity for surface layer breakdown is apparently reached north of Sta. B, with the associated breakdown in surface layer caused by massive turbulence and the subsequent downward mixing of fresh water.

3.2. FRESH WATER

Indian Arm has three main sources of fresh water: the Indian River which discharges at the head of the fjord; numerous peripheral streams which cascade down the fjord walls; and the discharge from the Buntzen power plant. The character and proportion of these primary sources combine to establish the annual cyclic pattern of fresh water input into the fjord.

Most British Columbia fjords also have one or more rivers which discharge near the head. The two main sources of river water are precipitation runoff, and snow and glacial melt waters. Examination of river discharge cycles shows that although wide variations do occur from year to year, a consistent pattern is usually apparent for a fjord. In fjords in which the main river is large and primarily taps glaciated regions, the river runoff has a maximum in June and July and a minimum in December and January. Fjords which receive rivers draining regions with little or no stored precipitation have maximum runoff from August through December, followed by a minimum runoff from April to July. Many gradations between these two types are noted (Trites, 1955; Pickard, 1961).

The Indian River, draining into Indian Arm, was unmetered during the period of this study, but data are available for the period from 1914 to 1922. On the basis of these data, the relation between Indian River and concomitantly metered rivers of similar runoff pattern has been calculated. The present runoff of these rivers was utilized to provide an estimate of the Indian River runoff during the time of this study. During the 1914 to 1922 period, the method provided an estimate of the monthly runoff of the river that varied on an average by 15% from the actual values. The greatest difference occurred in December, during the latter part of the period of winter rains.

In most cases the rivers contribute the major portion of fresh water input, but in some fjords peripheral streams play an important role. In the fjords that have been considered from this aspect, peripheral streams contributed from 20 to 65% of the total fresh water which enters the fjords (Trites, 1955). Except in local regions—that is, cells of high precipitation—the amount of fresh water contributed by direct precipitation is small relative to the amounts contributed by rivers and peripheral drainage.

Indian River drains an area of 121 sq km; the peripheral streams to the west and east of the fjord drain a total area of 44 sq km; and the fjord itself has a surface area of 13 sq km. A comparison of the annual precipitation data from the Britannia Beach and Ioco meteorological stations, located outside Indian Arm but within 33 and 4 km of its head and mouth respectively, shows good agreement (*Anon.*, 1956b; 1957b; 1958b; 1959b). The annual precipitation cycle is similar, and the total precipitation for the two stations differed by 10% during the time of this study. For the present purpose it is assumed, therefore, that precipitation is the same over the drainage area of Indian River and the drainage area of the peripheral streams. On this assumption, peripheral stream discharge has been estimated from Indian River runoff on a proportional drainage area basis. This will be a maximal estimate since a portion of the headwaters of the Indian River are in a region of higher annual precipitation than either Britannia Beach or Ioco.

Ignoring the stored precipitation, and assuming that 50% of the total precipitation drains into the fjord (Tabata and Pickard, 1957), it can be calculated on the basis of rainfall area that 66% of the precipitation which reaches fjord waters arrives as river runoff, 25% arrives as peripheral stream runoff, and 9% as direct precipitation. Thus, over an annual cycle, both peripheral streams and direct precipitation do contribute a significant proportion of the fjord's fresh water.

If little or no storage of precipitation occurred in the drainage area of the fjord, the Indian River outflow would be expected to follow closely the annual precipitation cycle. As shown in Fig. 8, this is not so. From December through March, river discharge lags behind precipitation, indicating that an appreciable portion of the precipitation is being stored in the drainage area. During spring and early summer, although the rate of precipitation decreases, the rate of river discharge increases. This is effected by the melting and release of the snow and ice which accumulated during the late winter months. During May and June, river discharge is at its maximum and precipitation is near the year's minimum. With

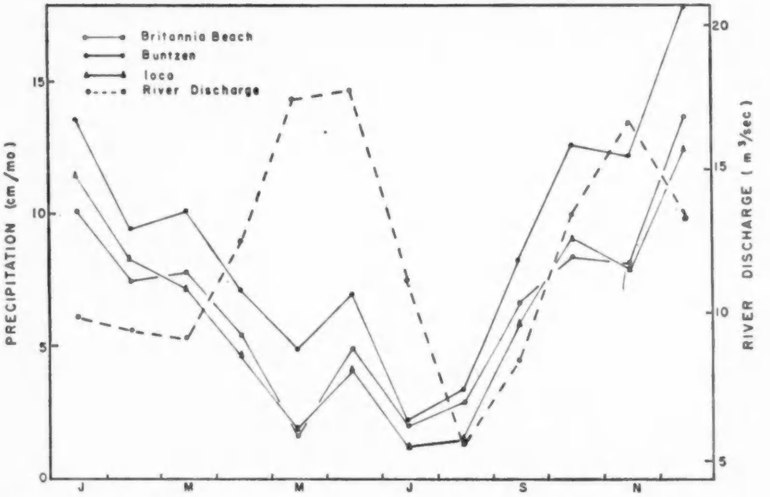


FIG. 8. Relation between mean monthly river discharge and precipitation (1956 to 1959).

the onset of winter rains, the precipitation and discharge curves fall into phase, indicating that the primary source of discharge during this period is direct runoff. Thus the bimodal cycle of river discharge results from the combination of two basic cycles: a spring peak primarily caused by melt waters, and a fall peak attributable to direct runoff.

In the 23 fjords which have been analyzed to date (Trites, 1955), the ratio between mean yearly fresh water discharge and unit area of fjord surface varies by a factor of about 10 (from 6.8 to 62.3 m^3 sec/km^2), the mean being about 19.1. Indian Arm has a mean yearly ratio of 9.5, placing it within, but toward the lower limit of that range. This is primarily attributable to the local climate of this fjord's drainage area. This region of the British Columbia Coast Range receives an average annual precipitation of 250 cm, while many of the drainage areas which are tapped by other fjord rivers and streams have figures in excess of 380 cm per year.

The fresh water sources of Indian Arm differ from those of other British Columbia fjords in one respect. Situated on the east side of the fjord opposite Sta. D is the Buntzen power plant. The water which is used by this plant is primarily collected from outside the drainage area of Indian Arm. In most respects the fresh water discharge from this plant can be treated as a large peripheral stream. It has one distinct advantage: data are available for the exact quantity of fresh water flowing out from this source. Based on the 37 observations each of river, peripheral, and Buntzen discharge indicated in Fig. 9, it is found that on an average, during a year this plant contributes 41% of the total runoff which, combined with that of the other peripheral streams, gives a

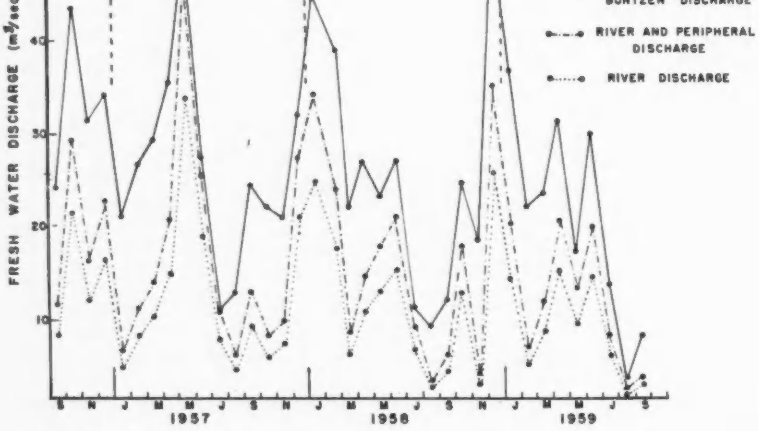


FIG. 9. Monthly mean discharge of fresh water into Indian Arm for primary sources (1956 to 1959).

sum peripheral runoff which is 58% of the total fresh water discharge into Indian Arm. This is within the range of 20 to 65% reported for other British Columbia fjords.

Under unusual meteorological conditions, low temperatures can freeze almost all the peripheral streams and drastically reduce the outflow of Indian River. At these times the primary sources of fjord fresh water are direct precipitation and Buntzen power plant discharge. At such times a high proportion of the fresh water entering the fjord is attributable to the discharge of the generating plant.

The location of the Buntzen power plant and the distribution of the major peripheral streams suggest that nearly 50% of the total fresh water which enters the fjord during the heavy winter rains enters at points well below the head. It should be noted that this is in contrast to most of the theoretical considerations of fjord circulation in which it is assumed that all fresh water entering the fjords is contributed by the river at the head (Pritchard, 1952).

3.3. TEMPERATURE

The primary processes which effect the changes in the heat content of the British Columbia fjord water masses are radiation–back radiation, condensation–evaporation, convection of sensible heat to and from the atmosphere, and advection. These combine to produce an annual cycle of temperatures with a single maximum and minimum. The cycle of surface temperature is in phase with the air temperature cycle, although of slightly lower amplitude. The annual temperature cycle in Indian Arm agrees in this respect. For selected depths the temperature observed during the three years are presented in Fig. 10, and a 3-year-mean cycle deduced from those is shown in Fig. 11.

The correlation between the air and surface water temperatures is close, both having minima occurring in January and maxima in August. These are similar to those of the British Columbia coastal waters where a minimum of 7.2±0.5°C is reached in January or February, and a maximum of 10 to 18°C in August (Pickard and McLeod, 1953). Throughout 5 months of the year, the air temperature exceeds the surface water temperature. During the remaining 7 months (fall and winter) the air temperature is less than the surface water temperature. At times when air temperature is higher than that of the surface water, the difference between the two is small. When the maximum surface water temperature is reached, the air temperature exceeds it by less than 1 C°. In months when the air temperature is less than that of the surface water, temperatures differ by more than 3 C°. This pattern of convergence during warming periods and divergence during cooling periods is probably associated with the stability of the water column, which in turn is associated with density. In general, the effects of radiation and sensible heat transfer are only important at the surface; subsurface heat transfer is accomplished chiefly by turbulent action. Quite apart from the effects of salinity variations, the warming of the surface results in lower densities and a more stable water column. Under these conditions, transfer of sensible heat from the atmosphere tends to produce a surface

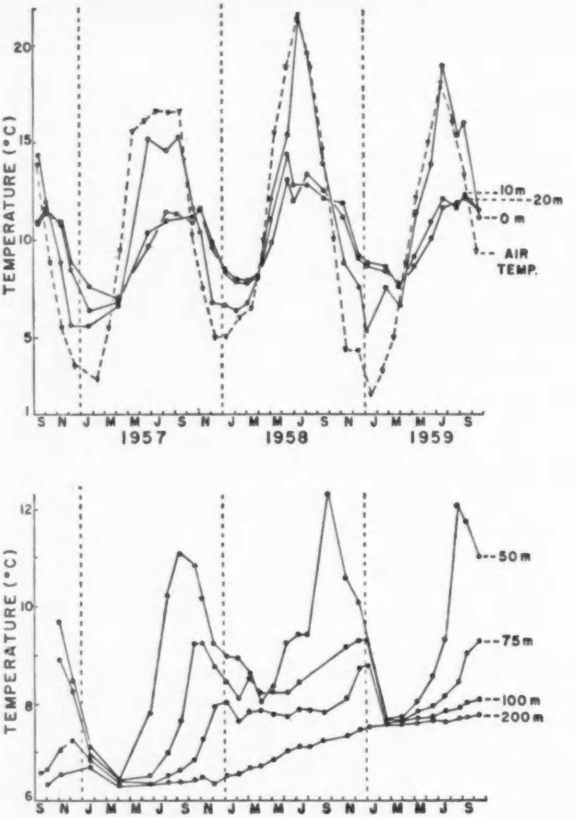


FIG. 10. Mean seasonal cycle of temperature at various depths (1956 to 1959).

water temperature comparable within 0.5 C° of the air temperature. Under cooling conditions, the surface waters become denser, which decreases the stability and brings about a movement of water away from the surface.

Seasonal fluctuations in temperature are evident to a depth of 75 m, and are less noticeable, though still apparent, down to 100 m. Figure 10 shows the typical recurring annual cycle of the seasonal fluctuations. Their character is determined by an occasional large intrusion of outside water. This occurs at intervals of some years. Between such instrusions, a slow, steady increase in temperature is evident. A layer with characteristics between these two regions occurs at approximately 100 m.

The curves for the mean temperature at 10, 50, 75, and 100 m show a gradual increase in the time of maximum relative to the surface waters. In addition, there is a suggestion of an increasing difference in time with increasing depth

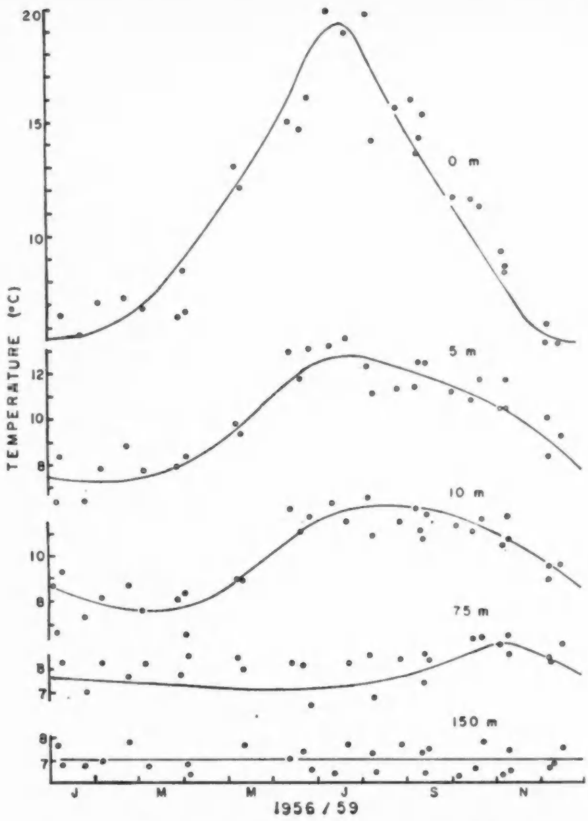


FIG. 11. Seasonal variations of temperature at Sta. D for various depths.

between the temperature minimum and maximum. The time of temperature minimum varies from January–February at the surface to March at 100 m. Thus the time difference between the minimum and maximum temperature is 6 months at the surface, but is 9 months at 100 m. This difference seems to indicate that the rate of downward cooling is 50% faster than the rate of downward warming.

This difference in the rates of heat transfer appears to be associated with changes in the intensity of vertical turbulent transport at different seasons. The stability of the water column is lowest during spring and early summer months and is greatest during late summer and fall. If one assumes that the rate of turbulent transport is inversely proportional to the stability of the water column, the downward transfer of the spring minimum would be speeded up and the downward transfer of the summer maximum would be retarded. Although the assumption is often made that the source of energy for such turbulence is derived from weak horizontal currents and tidal movements, it does not appear to be so in this instance. Since the horizontal temperature gradients are small relative to the vertical gradients, horizontal currents probably do not greatly influence the vertical temperature gradients.

In addition to distinct annual fluctuations, several other features are apparent in Fig. 10. Some of these features are:

a. The varying depths to which seasonal fluctuations occur during different years.

b. The long-term increase in deep water temperatures.

c. The consistency of time of temperature inversion from year to year.

During the spring of 1957 and 1959, sharp decreases occurred in the temperatures of the deeper waters. Two mechanisms could account for these decreases: the cooling of surface waters followed by an overturn of the water column, or an intrusion of colder water into the fjord. As a consequence of the large vertical salinity gradient, the stability in Indian Arm is such that overturn of the water column would be highly unlikely. Inasmuch as an increase in salinity occurred concomitantly with the temperature decreases and since there is no source of higher salinity water in the water column, an intrusion of outside water must have occurred at this time. The 1959 intrusion did not affect the established trend of an increase in bottom temperature, either because it did not reach the bottom waters or because the temperatures of the intruding waters were within 0.1 C° of the temperature of the bottom waters.

During 1958, such an intrusion either did not occur, or it was small in extent and effect, as evidenced by a small decrease in temperature at 75 and 100 m during February. Since a massive intrusion of colder water during early spring obscures the downward transfer of the surface temperature minimum, it is difficult to ascertain the maximum depth which this minimum attains. If one assumes that little or no cold water was introduced horizontally during the spring of 1958, the observed changes in temperature structure would be due primarily to vertical mixing. During this period, a clearly defined temperature minimum occurred at the surface in February, at 20 m in March, and at 50 m in April. At this time the temperature maxima was at approximately 75 m with a decrease in temperature both toward the surface conditions (with little or no inflow of outside water) the surface minimum does not extend deeper than about 75 m.

The dates of the spring temperature inversion are nearly the same in each of the three years. By linear interpolation, the date on which the spring inversion occurred was April 10 in 1957, April 3 in 1958, and April 11 in 1959. The fall inversion is just as consistent, with the interpolated dates being October 9 in 1957, October 4 in 1958, and October 17 in 1959. Both the spring and fall inversions for the three years occur within a range of 8 days. Such regularity suggests a remarkably consistent spring and fall surface radiation pattern. This is supported by the air temperatures; the mean monthly air temperatures (primarily influenced by the surface radiation pattern) from 1956 to 1960 were 9.6° for April and 9.7°C for October.

During the time of spring temperature inversion, the water column is virtually isothermal during a "normal" year. In 1957 and 1959 the mean temperature gradient from the surface to 200 m was 0.0035 and 0.0032 C°/m respectively. During 1958 a similar low vertical gradient of 0.0030 C°/m was present in the 0 to 75-m portion of the water column, but a much higher gradient of 0.01 C° existed between 75 and 200 m.

The fall temperature inversion is not accompanied by as strongly developed an isothermal pattern as the spring inversion. In all three years, isothermal conditions extended to a depth of about 30 m, with underlying portions of the water column having a much larger temperature gradient.

The summer maximum of surface temperature occurred nearly at the same time as that of air temperature. The maximum annual surface temperature varied by about 6 C° during the three years 1957 through 1959. In order, maxima were 15.5, 21, and 19°C. These followed the trend of monthly air temperature which had corresponding maxima of 17, 22, and 18°C.

A similar, though less well defined relation between the minimal temperatures of the air and surface water is evident. The temperature minimum of the surface water occurred during January in three years. The highest minimum was recorded 1958. This month also showed the highest air temperature minimum. The lowest surface minimum was observed during 1959. During January 1957 the mean air temperature was 1.1°C and the surface temperature was 5.60°C. Calm conditions during the cruise of January 1957 are probably responsible for the low minimum recorded at this time.

Surface ice was observed twice—once in January 1957 and once in January 1959. On both occasions the ice was thin and did not persist; it formed at the northern end of the fjord during the night and broke up during the following day under the influence of light winds. Residents at Buntzen Bay report that during particularly severe winters the fjord may be frozen over for several days from the region near Sta. D north to the head.

The monthly changes in vertical temperature structure are clearly shown when the temperatures at depths are plotted against time, as indicated in Fig. 12. The disruptive effects of the massive intrusion occurring in January through March 1957 are clearly evident (top panel of Figure). In 1959 a similar effect is apparent. Some concept of the relative extent of these two intrusions can be gained by comparing the vertical extent of the isotherms of these periods. In 1957 the intrusions appears to have virtually flushed the fjord, whereas in 1959 the more restricted vertical development suggests a more limited flushing. The effects of vertical mixing in spring and early summer can be seen in the downward sloping isotherms. A high temperature core is present between 10 and 35 m during August of each year. When the summer maximum (Fig. 11) is examined in detail, the top of this core is delimited by a temperature inversion at 10 to 20 m. This inversion was of short duration in 1957 and 1959, but lasted for 2 months in 1958. An examination of the longitudinal distribution of temperatures

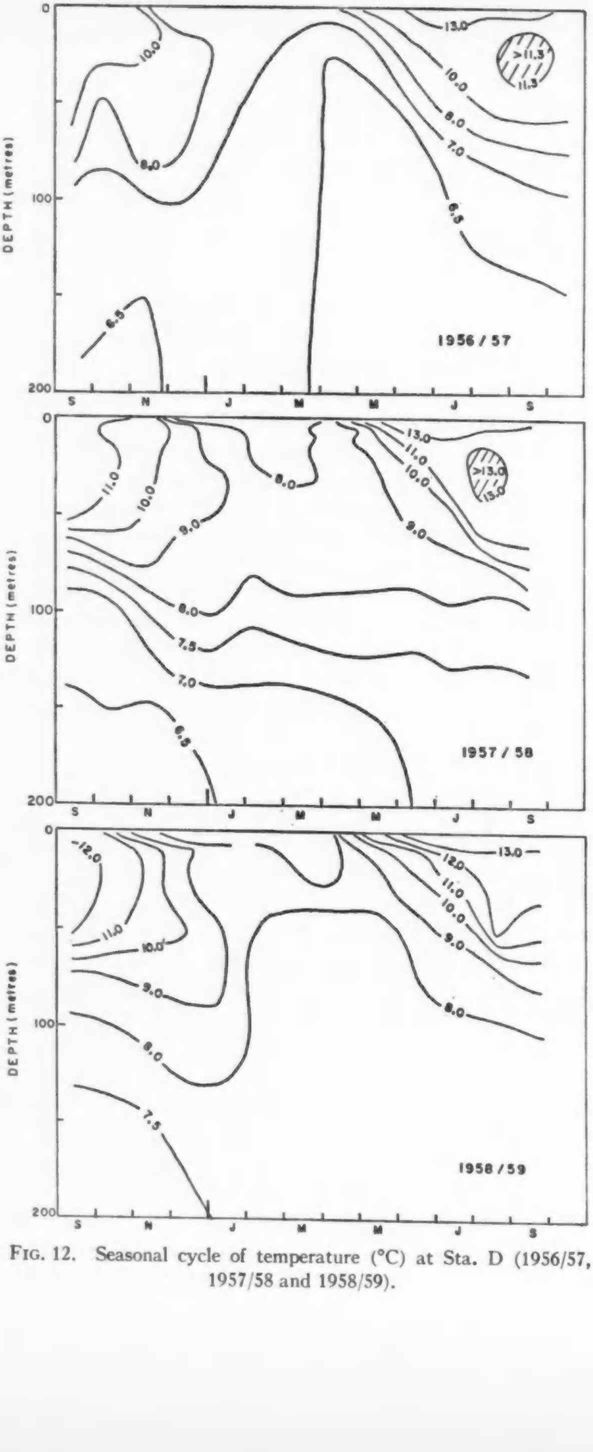


FIG. 12. Seasonal cycle of temperature (°C) at Sta. D (1956/57, 1957/58 and 1958/59).

prior to and during the summer, suggested there is an influx of outside water at 20 to 30 m depth. During July 1958 the vertical temperature gradient at all stations north of Sta. F showed a decrease in temperature inversion of 0.33 C° at 30 m. During August the inversion was evident from Sta. F north to Sta. B near the head. The greatest inversion (1.5 C°) occurred at Sta. D. At Sta. C it was 0.99 C° and at Sta. B, 0.92 C°. No trace of the inversion could be seen at Sta. A. The temperature inversion commenced at 5 m at Sta. F, and 7.5 m at the head, and had its center lying between 20 and 30 m.

During 1959, when the inversion was not as persistent nor as strongly developed, it could still be traced from the fjord mouth north to Sta. B. The depth at which it began was 10 m, but the maximum development occurred at 20 to 30 m. No trace of this inversion could be seen in the preceding July or the following September. It was either residual when observed in 1957 or very weakly developed and it was barely detectable in the central basin at Sta. E, D, and C.

An analysis of the data shows that this inversion pattern, beginning at the mouth of the fjord and developing northward at intermediate depths, is the result of a very slow inflow of outside water at 20 to 30 m. This slow inflow is a result of the pattern of tidal intrusion occurring during this season.

If the deep water is considered, a gradual increase in temperature occurred from April 1957 to October 1959. Throughout this period of 31 months, the temperature increased in every succeeding month except November 1958. The total increase was nearly 1.5 C°. Such a slow steady increase is attributable to downward mixing of warmer water which occurs in the absence of large intrusions of colder outside water. Under these conditions the deep basin water does not appear to be affected by conditions outside the basin. This provides an opportunity to determine accurately the rate of eddy diffusion, which will be discussed later.

The pattern of horizontal temperature distributions is not as clear as that for vertical distribution. The gradient in the fjord basin averaged less than 0.003 C°/km at 200 m, 0.01 C°/km at 150 m, and 0.04 C°/km at 100 m. The maximum gradient observed below 100 m exceeded 0.06 C°/km only once. In December 1957 a gradient of 0.12 C°/km was observed, apparently associated with a small intrusion of warm water at 100 m.

The largest gradients were observed in the surface layer during the midsummer maximum in association with periods of low runoff. At this time values were as high as 0.21 C°/km. During the remainder of the year gradients rarely exceeded 0.06 C°/km. At intermediate depths gradients were proportionally lower.

The direction of the gradients shows some consistency. Table I depicts the gradients at representative depths and indicates that the yearly trends fall into four groups: from January through March, the general tendency is for a decrease in temperature from fjord head to mouth; from July through September, for an increase in temperature from head to mouth; and in intervening periods of April–June and October–December there are less consistent patterns that vary from year to year.

TABLE I. Direction of horizontal temperature gradient at various depths.

Year	Depth (*metres*)	Month											
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1956	5	...	...	...	...	...	...	...	...	–	+	+	*
1957	5	–	...	...	–	+	–	...	*	–	*	*	–
1958	5	+	+	+	+	*	+	–	–	...	...	*	*
1959	5	*	*	*	...	*	*	–	–	...	*	...	...
1956	10	...	...	...	...	...	...	...	...	–	+	+	*
1957	10	*	...	...	–	+	–	...	–	–	*	*	*
1958	10	+	+	+	*	–	+	–	–	...	...	*	+
1959	10	+	+	+	...	*	*	–	–	...	*	...	...
1956	30	...	...	...	...	...	...	...	...	...	...	...	...
1957	30	...	...	...	...	...	*	...	–	–	*	*	*
1958	30	+	+	+	+	*	+	–	–	...	...	+	+
1959	30	+	+	+	...	*	–	–	–	...	*	...	...
1956	50	...	...	...	...	...	...	...	...	–	*	+	*
1957	50	+	...	...	–	–	+	...	–	–	*	–	*
1958	50	+	+	+	+	*	*	–	–	...	...	*	*
1959	50	+	+	+	...	*	*	*	–	...	–	...	...
1956	100	...	...	...	...	...	...	...	...	...	...	+	+
1957	100	–	...	–	–	...	–	...	–	–	*	–	–
1958	100	–	+	–	*	*	*	–	+	...	...	*	*
1959	100	*	+	+	...	+	+	–	–	...	–	...	...

– = Decreasing temperature trend mouth to head.
+ = Increasing temperature trend mouth to head.
* = No consistent temperature trend.

A strongly developed minimum in the vertical temperature distribution as reported in other fjords (Pickard, 1953) was not observed in Indian Arm. However, during the spring months of 1958 and 1959 well-defined maxima were observed at 50 to 75 m. The occurrence of these maxima might be attributed to the same basic mechanism which produces the minima noted in other fjords. In order to explain these features under ideal conditions the following model is presented.

At a time during late spring, when the water column is essentially isothermal and horizontal currents are negligible, the input of heat to the water column exceeds the loss, and gradual warming of the surface layer takes place. With continued warming and some vertical mixing, a characteristic summer pattern with high surface temperatures forms. These temperatures decrease with depth until the lowest temperatures are reached in the bottom waters. In early fall the loss of heat from the water column exceeds the heat input, resulting in a decrease in temperature of the surface layer. If the cooling process during the winter is of the same intensity and duration as the warming process during the summer, further cooling with associated convective and turbulent transfer of heat will again produce isothermal conditions from surface to bottom. Continued cooling produces typical winter temperature gradients, in which there is a minimum at the surface and an increase in temperature toward a maximum in deep water.

Since both cooling and warming processes of the water column originate at the surface, a point will be reached during the process of cooling when there is a temperature maximum at an intermediate depth; and conversely, during the warming process a temperature minimum will be reached at an intermediate depth. These maxima and minima will persist if they are strongly developed as a result of a particularly cold winter or warm summer; or if the warming process is longer and more intense relative to the bottom waters than the cooling process, and vice versa; or if the advective processes are weak during one season.

In Indian Arm two factors combine to prevent a well-defined persistent temperature minimum. The warming trend is much stronger relative to the bottom waters than is the cooling trend. This probably results from the warming period occurring chiefly during low runoff and high stability. Secondly, intrusions of outside water occur in February, which prevent the maximum development of the cooling trend.

The formation of the most clearly defined maximum is depicted in Fig. 13. The vertical temperature gradients are plotted for Sta. C at the northern end

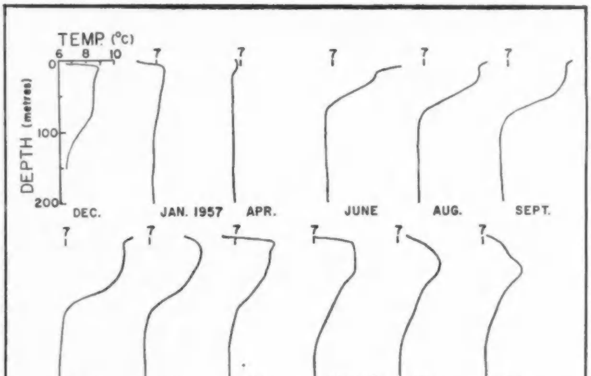


FIG. 13. Vertical temperature profiles for Sta. C (1956 to 1959).

of the fjord. This station is less affected by horizontal currents and tidal intrusions than more southerly stations. Isothermal conditions were present in April 1957, probably resulting from the thorough flushing of the fjord which occurred during the preceding months. In April, the first slight warming of the surface waters could be detected. Throughout succeeding months the warming trend intensified until the maximum was reached in October. In November, the surface layers had begun to cool and the cooling trend continued until March 1958. In March, the surface layer was again beginning to warm, and by April isothermal conditions were approached. However, the maximum attained during the preceding fall persisted throughout the cooling period, and could still be seen as late as May 1958. This same pattern was present during 1959, although it was partially obscured by an intrusion of cool water during February.

In longitudinal sections the dissipation of the temperature maximum in the southern end of the basin can be seen clearly. During the summer of 1957, the warming of the water column was apparent at all stations within the fjord. During the fall, the temperature maximum persisted as a high-temperature layer extending the length of the fjord. By November and December, the seaward end of this layer had been eroded, probably by horizontal currents resulting from tidal intrusions. The maximum thus developed the appearance of a high-temperature tongue extending seaward from the head of the fjord at intermediate depths. With succeeding months, the continued erosion of the seaward end of the tongue progressively reduced its length. In January, it extended only to Sta. D; in February, only to Sta. C; and by April the tongue remained strongly developed only at Sta. A near the head of the fjord. A strongly developed maximum can be considered as a conservative feature of the intermediate depths, and the rate of its erosion can be used to provide a measure of the water replacement pattern near the fjord mouth. However, since it is a seasonal pattern, such a measure would only hold true for a few months during the year.

Two local conditions may temporarily alter the temperature distribution in the fjord: a condition which produces a great deal of mixing, and the influx of large volumes of low-temperature water. Meteorological conditions can produce strong down-fjord winds which mix the upper layers of water. This condition reduces the temperature gradient in the upper layers, and may result in an isothermal condition. Cooling of the surface water near the entrance of rivers and streams may occur. This is particularly noticeable off the mouth of Indian River during the runoff of melt water. Since the runoff occurs during the late spring and early summer, this source of cold water tends to counteract the warming trend normally present at this time of year.

3.4. DENSITY AND STABILITY

Density (σ_t) and its effect upon stability has been to some extent examined by previous workers in British Columbia fjord waters. It has been demonstrated that variations in σ_t generally follow the variations in salinity closely enough to validate the use of salinity distribution patterns as an approximation of densities (Tabata and Pickard, 1957). Values of σ_t previously reported for these waters range from 0 at the head of the fjords with high runoff to 26.0 in deep basin waters.

The annual cycle of σ_t for selected depths in Indian Arm is presented in Fig. 14. A comparison between this annual cycle and the salinity cycle depicted in Fig. 4 indicates a gross similarity. The surface waters show a bimodal curve generally reaching maxima in May and October. At 5 to 50 m there is a unimodal curve with the maximum occurring progressively later with increasing depth. At 5 m the maxima usually occurs in June and at 50 m in September. Below 50 m no precise annual cycle exists. Figure 14 shows the sharp increase in densities which occurred during January through March 1957, followed by a slow steady decrease in density through 1959. This increase resulted primarily from a corresponding increase in salinity which in turn is attributable to an intrusion of saline water at this time. The lowest value (1.98) was encountered in May 1958 in the surface waters of Sta. A and the highest values (21.10 to 21.72) were found in the deep waters of the fjord basin.

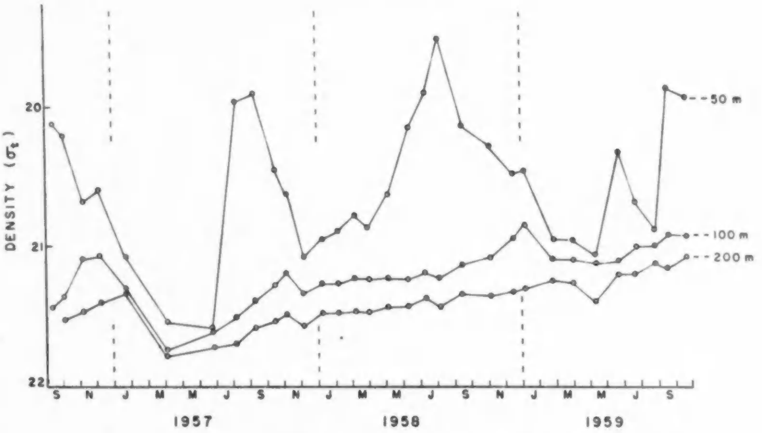


FIG. 14. Seasonal variation in density at Sta. D for various depths.

Of direct importance to dynamic oceanography is the influence of density distribution upon stability of the fjord water mass. The stability may be considered directly proportional to the vertical density gradient and can be expressed as:

$$E = 10^{-3} \frac{\mathrm{d}(\sigma_t)}{\mathrm{d}z}.$$

Stability values have been computed for the three years, and are presented as seasonal profiles in Fig. 15. As with temperatures and salinity, the distribution for 1957 and 1959 follow the same basic pattern; 1958 was an atypical year. During typical years, and to some extent during 1958, there was a tendency throughout the water column for a decrease in stability to occur during late winter and early spring, followed by an increase in stability with a maximum in June and July. The values of 10^8E through the water column range from about 150,000 to 400,000 m^{-1} at the surface to about 20 to 200 m^{-1} in deep basin water.

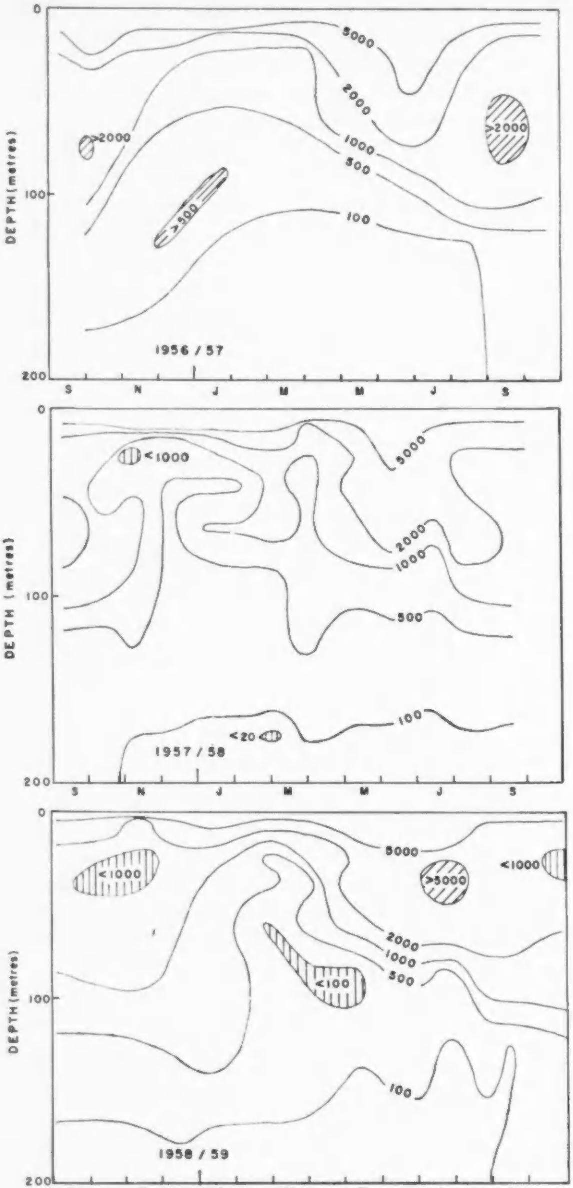


FIG. 15. Seasonal cycle of stability ($E = 10^{-3}\frac{d\sigma_t}{dz}$, in 10^{-8}m^{-1}) at Sta. D (1956/57, 1957/58 and 1958/59).

The stability shows a roughly exponential decrease with depth during most of the year. However, consistent exceptions occur which are probably associated with the circulation pattern of the fjord. During September, October and November, regions of low stability occur at depths of 20 to 50 m. While their intensity varied, these low stabilities were present during all three years. A similar pattern occurred in February to May of 1959 at 60 to 125 m depth. Since fluctuations in the density gradient initiated by a change in surface salinities and temperature produce only a progressive increase or decrease in stability, such inversions must have resulted from lateral intrusions of water with different density characteristics. These isolated regions of low stability suggest intrusions of outside waters. When the longitudinal profiles of the fjord are examined during these periods, such intrusions often appear as an up-fjord tongue of oxygen isolines. The strongest intrusion which occurred in the spring of 1959 is illustrated in Fig. 16.

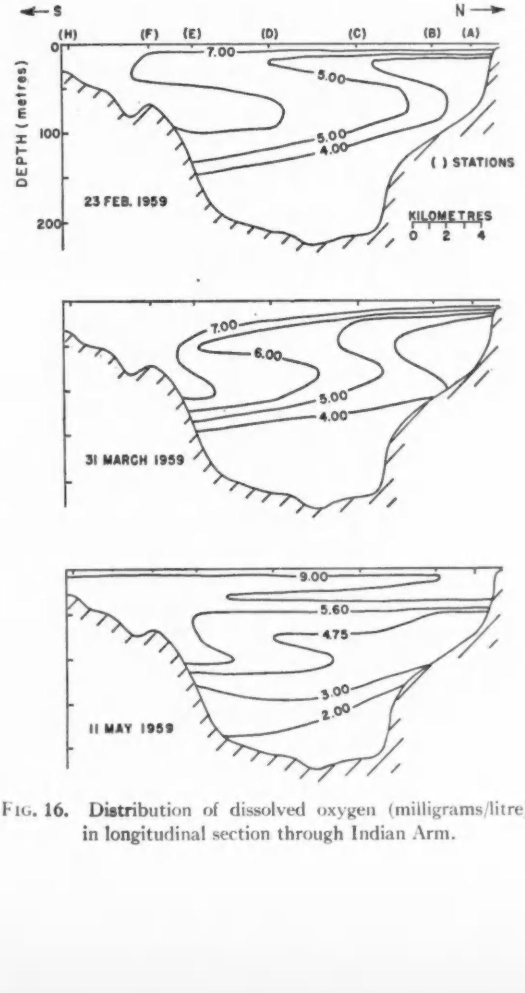


FIG. 16. Distribution of dissolved oxygen (milligrams/litre) in longitudinal section through Indian Arm.

In order to apportion the relative effectiveness of temperature and salinity in establishing stability, the temperature and salinity gradients based on values linearly interpolated to the 15th of each month were computed for three layers of water at representative depths. The gradients were then weighed according to their relative effect in establishing the stability. The results of these calculations are presented graphically in Fig. 17.

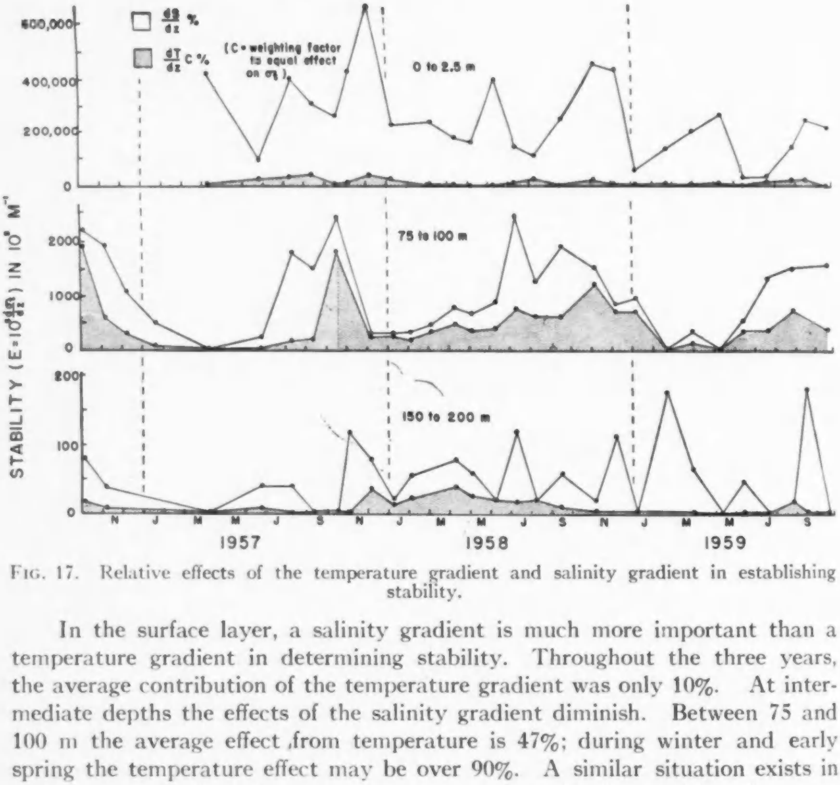


FIG. 17. Relative effects of the temperature gradient and salinity gradient in establishing stability.

In the surface layer, a salinity gradient is much more important than a temperature gradient in determining stability. Throughout the three years, the average contribution of the temperature gradient was only 10%. At intermediate depths the effects of the salinity gradient diminish. Between 75 and 100 m the average effect from temperature is 47%; during winter and early spring the temperature effect may be over 90%. A similar situation exists in the deep water, where the average temperature contribution is slightly less than 40%. Thus, for short periods, temperature may be the sole determiner of stability.

An important consequence of the role of temperature in determining stability is related to the delay in the occurrence of the summer maximum temperature at the surface, as shown in Fig. 10 and 11. This delay may produce a situation where the temperatures at the surface during the preceding summer determine the stability pattern of intermediate and deep waters during the following winter and early spring; for example, the unusually warm summer of 1958. By late fall of that year, high surface temperatures had established a sharp gradient in the surface layers; but as the temperature maximum and associated gradient were transmitted downward, this gradient progressively overshadowed the salinity gradient in establishing the stability. During late winter and early spring, the temperature gradient was 85% responsible for establishing the stability at intermediate depths, and in deep water the temperature gradient was solely responsible for the existing stability.

Thus, while the general pattern of σ_t conforms with that of salinity, it does not follow that the salinity is always the most important factor in establishing the stability pattern. At times, particularly in deep water, the stability is determined predominantly by the temperature gradient. In surface water during periods of low runoff, the temperature gradient may be as important as the salinity gradient in establishing the stability pattern.

3.5. EDDY DIFFUSION

Vertical mixing in Indian Arm results from convection, vertical turbulence, vertical advection, or a combination of these mechanisms; its presence is shown by the observed vertical transfer of such conservative properties as heat or fresh water. Convection is most strongly developed during periods of extreme winter cooling. At this time, surface cooling increases the density of the surface water to the point where it sinks beneath the immediately underlying waters. However, such convection is inhibited by any appreciable stability. Examination of the annual cycle of stabilities (see Fig. 15) suggests that at all times the stability in the upper layers is large enough to prevent any deep-reaching convection. Consequently, with the possible exception of deep basin waters, it is believed that convective vertical transfer of properties did not occur to any significant extent during the three years studied. The vertical transfer of properties was therefore most likely effected by eddy diffusion associated with vertical turbulence.

An approximation of the magnitude of eddy diffusion can be gained by considering the rate of vertical transfer of a property. If a time is selected when the advective transfer of a property is negligible, and if one assumes that the observed vertical transfer is due to turbulent transfer alone, then it is possible to calculate an eddy diffusion coefficient. This can be expressed as follows. Let A be the eddy coefficient, Q the flux of heat, T the temperature, P the flux of salt, S the salinity, z the depth, c the specific heat of the water, and t the time, then:

$$Q = cA_t \cdot \frac{\partial T}{\partial z} \qquad \ldots. (1)$$

$$P = A_S \cdot \frac{\partial S}{\partial z}. \qquad \ldots. (2)$$

By assuming that A is constant over the time and depth considered, equations (1) and (2) can be approximated for numerical analysis by the difference equations (Tabata and Pickard, 1957):

$$A_t = \rho \frac{\Delta T}{\Delta t} \left(\frac{(\Delta z)^2}{T_1 + T_3 - 2T_2} \right) \qquad \ldots. (3)$$

$$A_S = \rho \frac{\Delta S}{\Delta t} \left(\frac{(\Delta z)^2}{S_1 + S_3 - 2S_2} \right) \qquad \ldots. (4)$$

where T_1, T_2, T_3 and S_1, S_2, and S_3 are the temperatures and salinities respectively at equidistant depths, Δz is the distance above or below T_2 and S_2; and ρ is taken as 1 g/cm³.

During most of 1958, the distribution of properties within the fjord suggests that the water mass below 100 m was relatively undisturbed. Eddy coefficients have been calculated for these periods and are presented in Table II with A_t values from Bute Inlet (Tabata and Pickard, 1957).

TABLE II. Numberical values for eddy coefficient derived from observed variations of temperature and salinity.

Indian Arm					Bute Inlet (Tabata and Pickard, 1957)			
Date	Depth (*metres*)	E	A_t	A_s	Date	Depth (*metres*)	E	A_s
June–Aug. 1957	150	210	0	3.13	Aug. 1950	110	500	0.58
Feb.-Mar. 1958	150	220	0.71	2.68	Sept. 1950	110	300	1.25
Mar.–Apr. 1958	150	350	2.29	0	May 1951	90	700	0.23
Apr.–May 1958	150	210	1.37	17.15	Aug. 1951	90	1000	0.63
Aug.-Sept. 1958	150	220	1.04	3.62	Oct. 1951	130	500	0.55
Sept.-Nov. 1958	150	230	0.92	0.45	Aug. 1952	110	400	0.21
Nov.–Dec. 1958	150	300	1.03	1.12	–	–	–	–
Dec.–Jan. 1958	150	370	0.61	2.13	–	–	–	–
Jul.–Aug. 1959	150	180	9.31	6.82	–	–	–	–

E = Stability $\left(10^{-3}\,\frac{d\sigma_t}{dz}\right)$.

A_t = Eddy coefficient derived from temperature variations (g/cm/sec).

A_s = Eddy coefficient derived from salinity variations (g/cm/sec).

The approximation is commonly made that A_t equals A_s under conditions where eddy diffusion greatly exceeds molecular diffusion (Sælen, 1950). In Indian Arm the calculated values for A_t and A_s are several hundred times as large as would be expected if the observed mixing resulted from molecular diffusion alone. Therefore, it is assumed that if the observed mixing results from eddy diffusion alone, A_t will approximately equal A_s in the deep basin waters of Indian Arm. This is not the case; during April, for example, the difference was quite large. Some departure from the basic assumption has occurred, and the most likely explanation is that there was an occasional weak horizontal inflow of water (having temperature and salinity characteristics different from the fjord waters) from outside. These weak inflows would not be readily identifiable by the distribution of properties alone. Conversely, periods with close correspondence of A_t and A_s suggest that the deep water was virtually undisturbed between the times of observations. During these periods, determinations of changes in non-conservative properties within the fjord can be made on the assumption that the observed changes were not influenced by advective processes.

The somewhat higher A_t values in Indian Arm compared with those under similar stability conditions in Bute Inlet suggest that turbulence may be a more important feature in the vertical mixing of deep water in the former than in larger British Columbia fjords such as the latter. This is most likely associated with the shallow sill and the narrows. Such features contribute to a more intense tidal pulse which supplies the necessary energy for the higher levels of turbulence.

3.6. Circulation

The circulation pattern of Indian Arm is dominated by one basic factor: the interchange of water between the basin and the adjoining water mass is restricted to depths at or above the sill. If the conditions in adjoining water masses were constant, the distribution pattern of conservative properties would be uniform and constant from sill depth to the bottom of the basin, and similar to those existing at sill depth in the adjoining water mass. Above sill depth, these would be continuous with those of adjoining waters.

Departure from this basic pattern is primarily due to two features: the fluctuating fresh water inflow, and the wide variations of properties occurring in adjoining water masses. These variations occur with regular and irregular time scales, the regular cycles ranging from diurnal to several years. The intrusions in and mixing of these waters with the fjord water mass produce the observable changes in the properties.

The main driving force for fjord circulation is the inflow of fresh water from the river and from peripheral streams. This accumulation of less dense water toward the head of the fjord results in a seaward slope of the water surface which induces a seaward movement of brackish water. The seaward movement of this surface brackish layer entrains more saline water from the underlying water mass. Continuity considerations require that there is a compensating movement of water into the fjord at some sub-surface depth. The resulting basic pattern is a two-layer system with net outflow on the surface and net inflow at intermediate depths. This basic pattern is characteristic of most fjords, and modifications of it occur in both British Columbia and Norwegian fjords. Most of these modifications are associated with the relation between the depth of the sill and the thickness of the brackish surface layer. If the depth of the sill is equal to or less than the thickness of the brackish surface layer, stagnant conditions result with a marked restriction in flushing of the fjord (Strøm, 1939). None of the investigations conducted in mainland British Columbia fjords to date have shown this extreme type of stagnant condition (*Anon.*, 1955–1959, 1956a–1959a).

Superimposed upon the basic circulation pattern are the effects of tidal action. While the net tidal flood must equal the net tidal ebb, a particular tidal cycle usually shows some asymmetry. Thus, all the ebbing waters may not be returned by the following flood, and vice versa. This temperary retention of a portion of the total tidal inflow for approximately 6 hours permits a small amount of mixing of the adjoining waters with fjord basin waters, with the result that a portion of the fjord water mass is renewed during each tidal cycle. The amount of flushing produced by this mechanism is usually small compared to the flushing action produced by entrainment.

While the circulation pattern of Indian Arm is the result of many different processes, the total circulation can be most clearly seen if it is resolved into two basic components, horizontal movements and vertical movements.

In common with almost all fjords, the main horizontal movement in Indian Arm consists of a surface outflow of brackish water, driven by the accumulation of fresh water within the fjord. The net amount of fresh water entering the fjord is the sum of the river runoff, peripheral stream runoff, discharge from the Buntzen power plant and direct precipitation, less that lost by evaporation.

The mean annual precipitation at the Buntzen power plant opposite Sta. D, which is halfway up the fjord, is 275 cm/year. If this precipitation rate is assumed to be representative of the entire fjord, the mean annual contribution by precipitation over the entire fjord north of the narrows would be 49.6×10^6 m^3/year. The total annual estimated evaporation is 4.4×10^6 m^3/year. Thus the excess of precipitation over evaporation, converted to mean transport out of the fjord, would be approximately 1.1 m^3/sec. Therefore, with the excess of precipitation over evaporation averaging less than 5% of the total runoff, the fresh water inflow into the fjord can be considered due to runoff alone.

The estimated mean monthly runoff of Indian River is shown in Fig. 9, with estimates of the additional fresh water contributed by peripheral streams and the Buntzen power plant. This inflow is dominated by the bi-yearly peaks previously discussed. Apart from short-term tidal fluctuations, the amount of water in the fjord remains relatively constant. Thus, stability factors require that most of this fresh water be removed by the seaward flow of the surface brackish layer. A small portion of the fresh water mixes downward and temporarily remains in the fjord. Therefore, the total transport out of the fjord equals the total fresh water inflow plus any entrained water.

There is a general increase in salinity from the head toward the mouth of the fjord, indicating that the seaward movement of fresh water has entrained portions of the underlying salt water. This increase in salinity ranges from 3 to 5‰ during the fresh water minima to 15‰ during the maxima. If the salinity of the outflowing water at a particular point is known, and if the salinity of the entrained water is known, it is possible to calculate the total transport to this point knowing the fresh water inflow. This can be expressed as follows. Let X_0 be the head of the fjord and T_0 the total transport at X_1. If S_0 is the observed salinity of the outflowing surface layer at X_1, S_e the mean salinity at the depth of the entrainment between X_0 and X_1, and D the total amount of runoff entering between X_0 and X_1, the total transport toward the mouth at X_1 will be:

$$T_0 = D \frac{S_e}{S_e - S_0}. \qquad \ldots. (5)$$

The difference between the total transport and the fresh water runoff will represent the compensating volume of water which enters the fjord at some subsurface depth.

Direct current measurements indicate that at the depth where no net motion occurs, salinities average approximately 90% of base salinity. The monthly rates of total transport out of the fjord at Sta. F and at the narrows have been calculated using this depth as an approximation of the depth of entrainment.

From these net transport volumes it is possible to calculate the theoretical net currents at Sta. F and at the narrows. Using the assumed depth of entrainment as the depth of no net motion, these values ranged from 0.3 cm/sec during the years of inflow minimum to 8 cm/sec during the inflow maximum. Corresponding values at the narrows are 1 and 27 cm/sec respectively.

The horizontal water movements, which are net currents resulting from the outflow of fresh and entrained waters on the surface, vary according to the state of the tidal ebb or flood. On a flooding tide, the outflowing surface current is retarded, causing an accumulation of surface waters within the fjord. During the ebbing tide, the accumulated surface waters contribute to the velocity of the outflowing surface waters. Direct observations, and one 40-hour series of current measurements during a month having 27 m^3/sec fresh water inflow, suggest that the surface outflow is completely stemmed only during periods of low runoff. As a consequence, the tidal exchange normally takes place at depths below the surface brackish layer.

The tides in Indian Arm are of the declinational type. In common with most deep estuaries, the high and low tides occur virtually simultaneously throughout the length of the fjord, suggesting that the tides act primarily as a pulse at the mouth of the fjord (Dawson, 1920). The tidal amplitude ranges to 4.6 m during spring tides, with a mean amplitude of approximately 3 m. If one assumes that the tidal current is uniform across a particular section of the fjord and varies sinusoidally, then an approximation of the tidal currents at various tidal stages can be calculated. This can be expressed as follows. Let V_s be the tidal velocity at section X_1 during tidal stage s. If A is the surface area up-fjord of X_1, and a_s the cross sectional area at X_1, and dh/dt the rate of change of sea level at tidal stage s, then:

$$V_s = \frac{A}{a_s} \cdot \left(\frac{dh}{dt}\right)_s \cdot \qquad \ldots . (6)$$

Calculations for tidal velocities for various tidal amplitudes and tidal stages are presented in Table III. These approximations show tidal currents that reach 50 cm/sec at the narrows. The frictional effects of the sides and bottom of a fjord probably insure that the flow through the fjord is not laterally uniform. These effects are most pronounced in extremely restricted sections such as the narrows. Thus the calculated tidal velocities are considered minimal.

TABLE III. Calculated tidal current velocities for various tidal amplitudes and stages.

Tidal amplitude	Tidal stage			
	1/8 flood	1/4 flood	3/8 flood	1/2 flood
metres	*cm/sec*	*cm/sec*	*cm/sec*	*cm/sec*
2	10	17	23	25
3	14	26	35	37
4	19	35	47	50

Tidal velocities at the narrows play an important role in the dynamics of fjord circulation. Both as a consequence of the reversing actions of the tidal currents and of the velocity gradient existing between the two layers, intense turbulence can develop which effectively mixes portions of the surface and deeper layers of water. This results in two different types of water entering the fjord. When high-velocity gradients between the surface and underlying water exist, appreciable volumes of intermediate depth water (Fig. 18, layer c) are formed and enter the fjord. Because of its intermediate density it will probably enter just beneath the surface layer. The results of such inflow can be seen clearly in the annual cycle of salinities at 2.5 m, as previously discussed. The remainder of the underlying layer (Fig. 18, layer b) flows into the fjord in the form of a tongue along an isopycnal surface. During periods of low velocity gradient, either at the beginning and end of the flooding tide, or during low fresh water runoff, all the inflow moves into the fjord basin and flows up-fjord at a depth appropriate to its density. Such intrusions are often apparent in the distribution of various properties, as shown in Fig. 19.

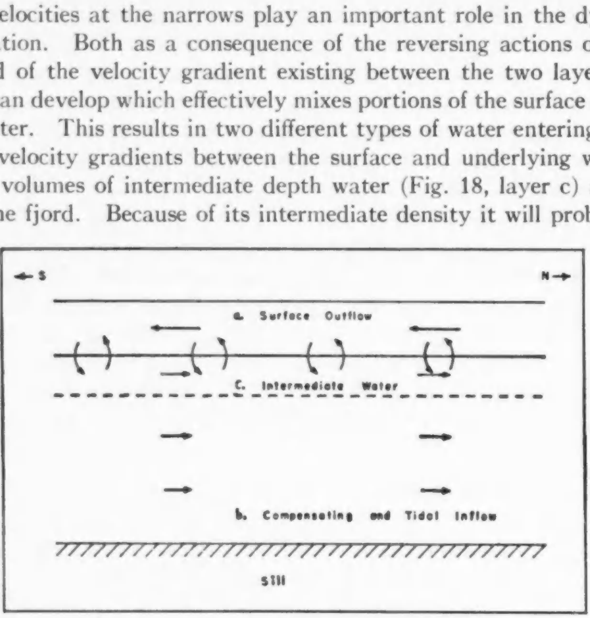


FIG. 18. Schematic illustration of mixing between the surface and underlying waters of the narrows.

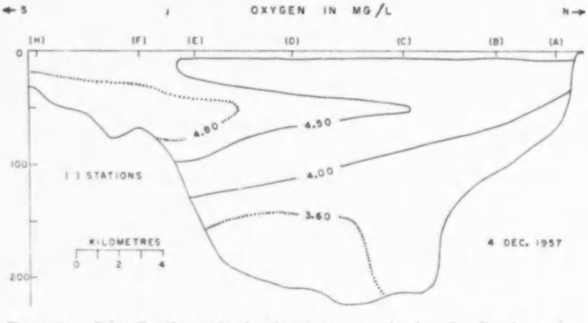


FIG. 19. Distribution of dissolved oxygen in longitudinal section through the fjord December 1957.

The development and maintenance of such tongues can be explained by considering the mechanism of tidal exchange in Indian Arm. It is hypothesized that the physical restrictions of the narrows, the density structure within the basin, and the associated high current velocities all combine to force the water flowing in during a flooding tide to take the form of a jet, as shown in Fig. 20a. During the ebbing tide there is no comparable restriction and the outflowing water is drawn from a comparatively wide depth range, as shown in Fig. 20b. Consequently, there is a net addition of outside water during each tidal cycle throughout the depth represented by the tidal tongue (Fig. 20c). These form and maintain the characteristic tongue which demarks the inflowing waters.

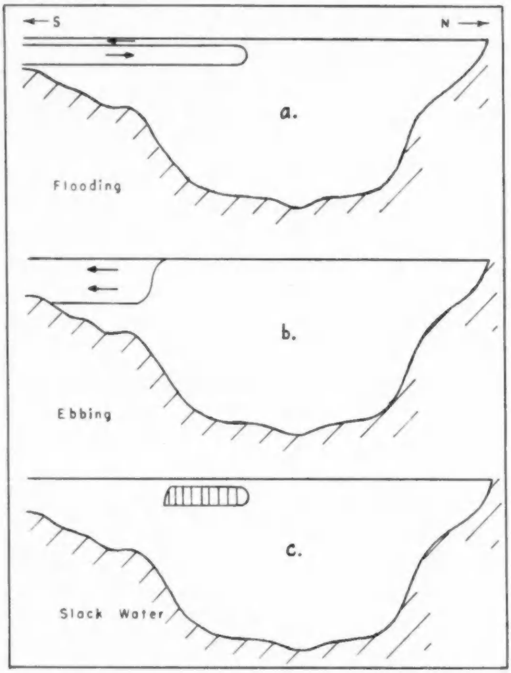


FIG. 20. Schematic illustration of the effects of tidal exchange between the fjord and neighbouring waters.

In order to demonstrate the tidal formation of this tongue, a series of hydrographic stations was occupied on the sill and north into the basin during different periods. In each series, temperature, salinity, and dissolved oxygen were determined at standard depths at four stations. At this time the difference in dissolved oxygen content between outside waters and the basin was larger than any of the other properties measured. Oxygen isopleths have therefore been plotted in order to show the tidal inflow (Fig. 21). The distribution of isolines during the middle of the ebb is shown in Fig. 21a. The nearly vertical position of the 5.75

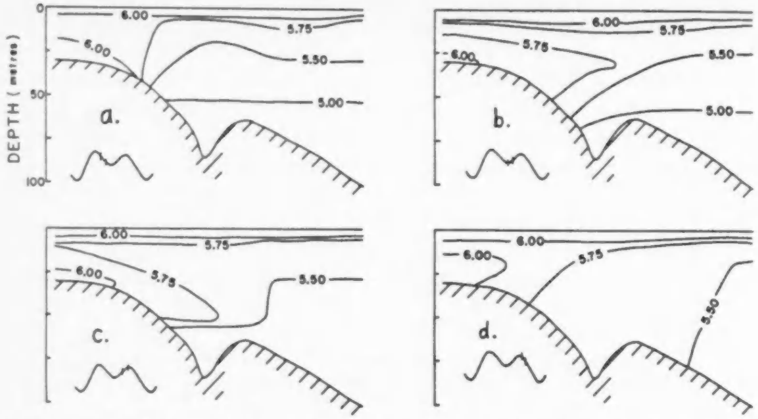


FIG. 21. Distribution of dissolved oxygen (milligrams/litre) in longitudinal section across the fjord sill: a, ebbing tide; b, flooding tide; c, flooding tide; d, ebbing tide.

mg/l isopleth and the slope of the 5.50 mg/l isopleth suggest that most of the water between 5 and 50 m moves seaward *en masse*. In Fig. 21 b, c the tongue of inflowing tidal water during early and late flood stages is evident. Figure 21d shows the condition at the beginning of the following ebb. The resulting up-fjord tongue is presented in Fig. 22, a longitudinal plot of the entire fjord basin.

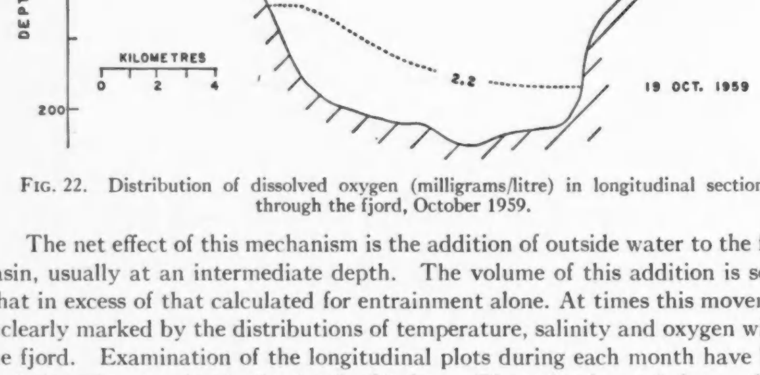


FIG. 22. Distribution of dissolved oxygen (milligrams/litre) in longitudinal section through the fjord, October 1959.

The net effect of this mechanism is the addition of outside water to the fjord basin, usually at an intermediate depth. The volume of this addition is somewhat in excess of that calculated for entrainment alone. At times this movement is clearly marked by the distributions of temperature, salinity and oxygen within the fjord. Examination of the longitudinal plots during each month have been made in order to estimate the depth of inflow. These depths, and the northernmost extent of these inflows, are presented in Table IV. During months when

TABLE IV. Seasonal variation in the horizontal extent and depth of intrusions of outside waters.

Year	Property		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1956	O_2	northward extent	...	...	...	...	...	...	...	...	Sta. D	Sta. A	Sta. A	Sta. F
		depth range	...	...	...	...	...	...	...	...	50	150	50	50
	Temp.	northward extent	...	...	...	...	...	...	...	...	Sta. E	Sta. E	...	Sta. F
		depth range	...	...	...	...	...	...	...	...	30–50	150	...	50
1957	O_2	northward extent	Sta. D	...	...	Sta. D	...	Sta. C	...	...	Sta. C Sta. F	Sta. D	Sta. D	Sta. C
		depth range	50–200	...	...	100–150	...	75	...	...	10 30–50	30–50	10	50
	Temp.	northward extent	...	...	...	...	...	...	...	...	...	...	...	...
		depth range	...	...	...	...	...	...	...	...	...	...	...	...
1958	O_2	northward extent	Sta. E	Sta. E	Sta. D	Sta. D	Sta. E	...	...	Sta. F	...	...	Sta. E	Sta. E
		depth range	30–75	30–50	30–75	30–75	50–75	...	...	30	...	...	10–50	10–75
	Temp.	northward extent	Sta. E	Sta. D	...	Sta. D	Sta. F	Sta. E	Sta. E	Sta. F	...	...	Sta. E	Sta. E
		depth range	30–75	30–50	...	30–50	20–30	30	10–30	10–30	...	...	10–50	10–100
1959	O_2	northward extent	Sta. D	Sta. B	Sta. D	...	Sta. D	...	Sta. E	Sta. C	...	Sta. C	...	...
		depth range	10–50	30–100	30–100	...	75–100	...	10–30	10	...	30–50	...	...
	Temp.	northward extent	Sta. F	...	...	...	...	...	Sta. F	Sta. D	Sta. F	Sta. E	...	...
		depth range	10–30	...	...	...	...	...	10–50	30–50	10–30	30–50	...	...

there was no clear evidence of inflow at an intermediate depth, even though the characteristics of the water at the sill suggested that such an inflow might be detected, it is assumed that the inflow occurred chiefly just beneath the brackish surface layer. The combination of a rough quantitative estimate of the amount of entrained water, and a qualitative estimate of the extent and depth of inflow, provides an approximation of the horizontal circulation of the fjord.

4. DISTRIBUTION OF NON-CONSERVATIVE OCEANOGRAPHIC PROPERTIES

4.1. Dissolved Oxygen

The pattern of dissolved oxygen distribution in Indian Arm is much more variable than that of temperature and salinity, since the concentration is influenced by biological activity. The major factors which bring about an increase in oxygen are diffusion from air to water; production by photosynthetic organisms; introduction in water from rivers and peripheral streams; introduction from intruding water masses of higher oxygen content than corresponding fjord waters. Those processes which decrease oxygen concentrations are respiration by living organisms; utilization in chemical oxidative processes; diffusion from water to air; seaward transport in the surface layer.

The most effective processes which increase the dissolved oxygen level tend to occur in surface waters; most of the processes tending to lower the oxygen level occur in deep water. Consequently, the vertical oxygen distribution usually ranges from somewhat more or less than 100% saturation at the surface to quite low values in deep water.

In common with other British Columbia fjords having low runoff, Indian Arm shows great variation from year to year in the distribution of dissolved oxygen. The measured values at selected depths at Sta. D are shown in Fig. 23. Two features of these distributions are conspicuous: a nearly unimodal cycle evident at 2.5 to 50 m and a long-term decreasing trend in deeper water.

The curves depicted in Fig. 23 have two components, a maximum which occurs in the spring of each year, and a much smaller overlapping maximum which occurs in the fall. During 1957 and 1958, the spring maximum developed in April and May, and was the larger of the two maxima. In 1959, the fall maximum appeared to be the larger of the two. While this may be an artifact introduced by the time of observation, it is considered unlikely when the duration and intensity of the preceding spring maxima in 1957 and 1958 are compared with the cruise schedule of spring 1959. It is unlikely that a well-developed spring maximum was missed. The mean annual cycle for the surface and intermediate depths is illustrated in Fig. 24.

The deep-water dissolved oxygen concentrations show a long-term tendency to decrease between periodic complete flushings of the fjord. This decreasing trend is broken by short-term seasonal increases, which usually occur during the spring of the year. The unusually high oxygen concentrations present in September 1956 are difficult to interpret because earlier data are lacking. These values decreased to a low of 4.5 mg/l in January of 1957. Between January and April, a large subsurface inflow raised oxygen values in the deep waters to the

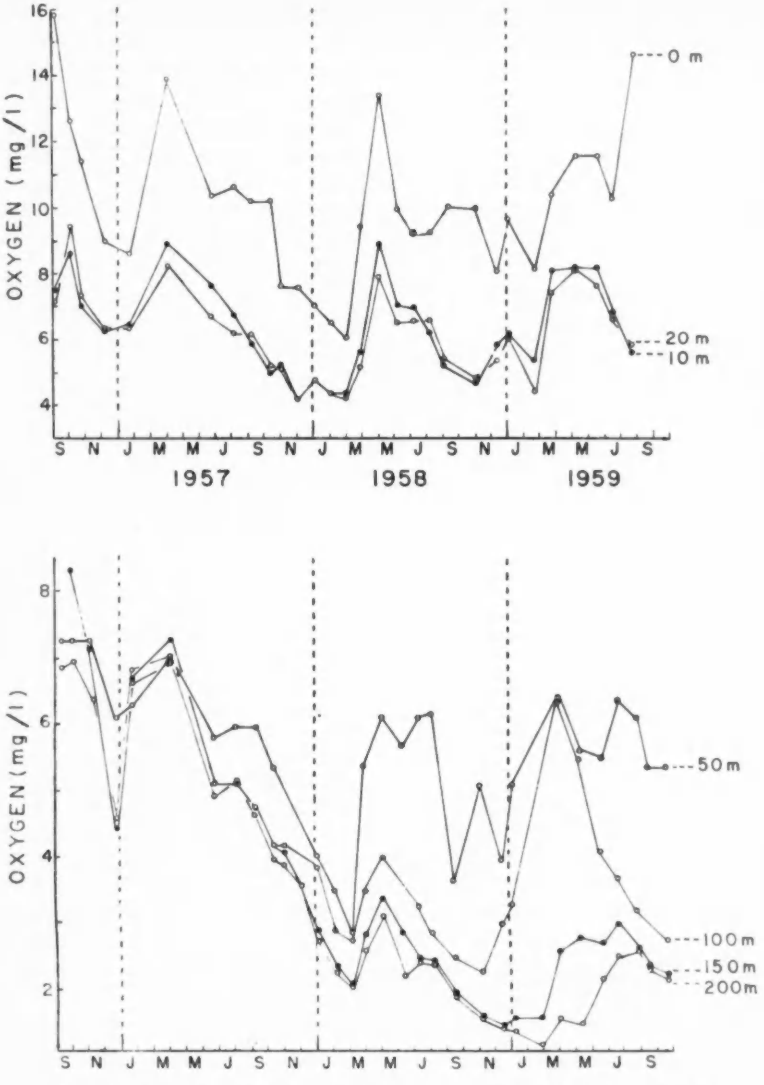


FIG. 23. Seasonal variation in dissolved oxygen in Sta. D for various depths.

highest levels (values exceeding 7.00 mg/l) noted. These decreased consistently to 2.1 mg/l during March 1958. At this time, another inflow increased the deep-water oxygen, which reached 3.2 mg/l by May 1958. This was followed by another consistent decrease lasting until March 1959, when a low of 1.1 mg/l was observed. This latter value is equivalent to 10% saturation, and is among the lowest noted in any mainland British Columbia fjord, since very few have oxygen concentrations less than 30% saturation in deep water (on occasion, essentially zero concentration has been encountered in the deep water of a fjord). The deep-water oxygen concentration is one of the primary differences between British Columbia and Norwegian fjords. In the latter, low oxygen values and associated stagnant conditions are frequently present. In general, oxygen concentrations in British Columbia fjords decrease with depth down to 200 m, where there is 40 to 60% saturation. From this depth to the bottom there is little change (*Anon.*, 1951–1955, 1956a–1959a).

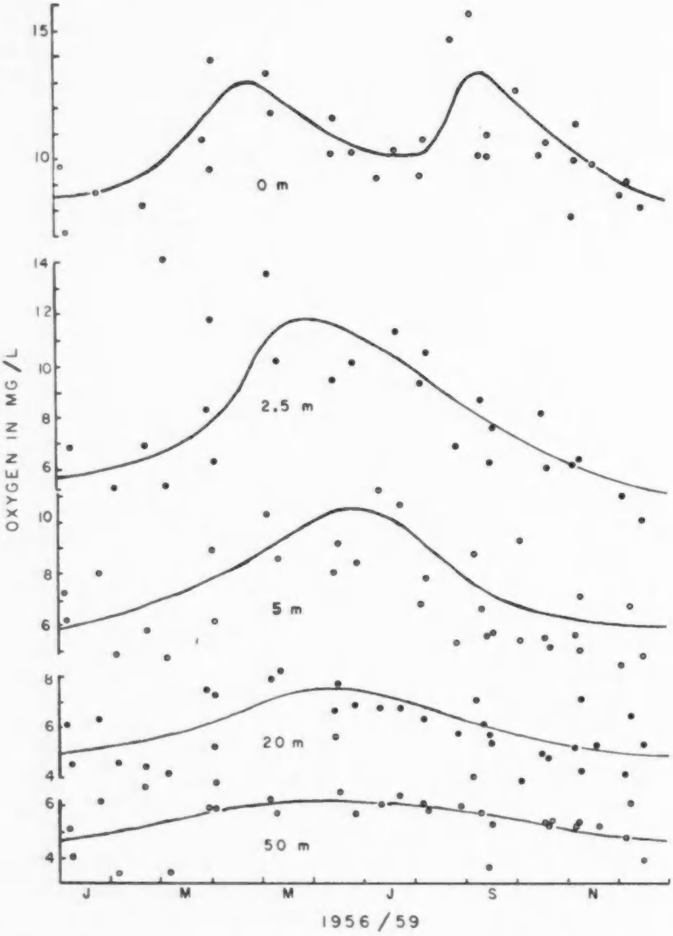


FIG. 24. Mean seasonal cycle of dissolved oxygen at various depths at Sta. D (1956 to 1959).

The oxygen distribution pattern in Indian Arm suggests that deep basin water is relatively undisturbed from March through December of each year. This view is supported by related temperature, salinity and density data. It thus provides an opportunity to establish the rate of oxygen consumption by respiratory and oxidative processes.

The longitudinal pattern of dissolved oxygen distribution in surface and subsurface layers is difficult to establish. There is a noticeable tendency for values to increase from head to mouth during winter and to decrease from head to mouth during summer. Moreover, the highest oxygen values observed during the spring and fall were at the head of the fjord. These usually ranged from 100 to 150% saturation, but during 1957 they were as high as 250% saturation. This value, observed on April 4, greatly exceeds the highest values previously reported for other British Columbia fjords (*Anon.*, 1951–1959). Values in excess of 200% saturation are unusual. In April 1957, the mass of high-oxygen water extended from the head south to the region between Sta. B and C, and was confined to the upper 2 m. By May 23, oxygen concentrations had decreased to 94% saturation. Excessively high values are probably associated with extremely intense and short-term phytoplankton blooms.

Both surface and subsurface maxima and minima of dissolved oxygen concentrations may result from several different causes. One can distinguish maxima which are due to biological activity and others which result from an influx of water with high oxygen concentration from outside the fjord. Those due to biological activity usually exist at shallow or intermediate depths and spread southward from near the head of the fjord. Maxima which result from an influx of high-oxygen water may occur at any depth in the fjord and spread northward. A third type of maximum can result from the influx of low-oxygen water at intermediate depths and produces the appearance of a high-oxygen core at greater depths.

The origin of dissolved oxygen minima may also be either kinematic or biological. A low-oxygen layer can develop from the decomposition of organic material which is slowly sinking following a bloom at the surface. A low-oxygen core can result from an influx of low-oxygen water or an influx of high-oxygen water near the bottom producing the appearance of a low-oxygen core in intermediate depths.

Two features of the upper 30 m which recur each year are a shallow minimum at the mouth in fall and a shallow maximum at the head in spring. The maximum is apparently biological in origin, whereas the fall minimum is probably associated with circulation.

In about May of each year, a dissolved oxygen maximum forms at about 2.5 m near the head of the fjord. The maximum appears to be related to the spring phytoplankton bloom, and at times can be traced to the mouth of the fjord. The extent of the maximum varies from year to year. In 1957 a maximum of 112% saturation was observed at 2.5 to 5 m. In 1959 a maximum of 145% saturation occurred in June and had its strongest development at the head of the fjord. This maximum could be traced seaward to Sta. E and was most intensively developed between 2 and 3 m depth. The most extensively developed maximum occurred in 1958 (Fig. 25, top and middle panels). The concentration began in April, reached 150% saturation in May, and gradually tapered off.

The second recurring feature of the shallow waters is a minimum which occurs during August and/or September of each year. This ranges from 10 to 20 m depth, and during its most pronounced development extends from the sill north to about Sta. C (Fig. 25, bottom panel). In 1957 and 1959 the minima were similar in intensity and extent, occurring during September and August respectively.

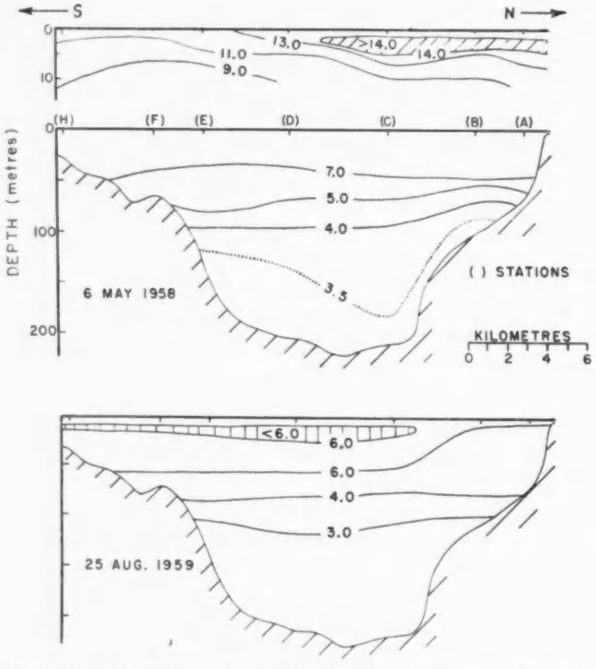


FIG. 25. Distribution of dissolved oxygen (milligrams/litre) in longitudinal section through the fjord, May 1958. (top and middle panels) and August 1959 (bottom panel).

The strongly developed minimum near the mouth of the fjord suggests the intrusion of a tongue of outside water with low oxygen concentration. It is a short-term feature, however, and was never observed to persist for more than one month. A low-intensity residual minimum, no longer continuous with outside water in the region of the sill, usually can be observed during the following month.

Both of these features support the conclusions reached in the foregoing discussions on other oceanographic properties: that 1957 and 1959 are similar in pattern and represent typical years, while 1958 represents an atypical year. The difference observed in these years also suggest that an indication of factors contributing to the extensive development of the shallow maximum in 1958 may be found by comparison of the general oceanographic features of 1957 and 1959 with those of 1958.

When the distributions of the other oceanographic properties were examined, several features were apparent. The period May through July 1958 had intermediate levels of river runoff, between a high in 1957 and 1959. However, examination of surface temperatures focuses attention upon the unusually early increase in surface temperatures in 1958. During 1958 the highest surface temperature (21°C) of the three years was recorded (Fig. 11). High temperatures extended to depths of more than 50 m at this time. The surface light intensities measured during the cruises of 1958 were higher than those measured during corresponding periods in 1957 and 1959. Therefore the greater development of a phytoplankton population was probably encouraged by the warmer temperatures and high light intensities. Moderate runoff, and comcomitant small entrainment of water and contained phytoplankton, would have permitted such a population to develop more fully than was possible during corresponding periods of 1957 and 1959.

Both maxima and minima can be seen at greater depths and it is difficult to determine which is the more important. When a maximum occurs there are two associated minima, unless the maximum occurs at the bottom. In this discussion, attention will be centered upon the maximum or minimum which seems to have originated at the mouth of the fjord. Formation at the mouth of the fjord implies that the maximum, or minimum, is associated with intrusions of outside waters, and in most cases this is supported by temperature and salinity data. One exception to this occurred in 1959.

In May 1958, a well-developed maximum was observed which extended from the head of the fjord south to about Sta. E (Fig. 25). This tongue of high oxygen concentration occurred at 25 to 30 m, with its strongest development at the head of the fjord, gradually decreasing toward the mouth. It appears to have its source in a center at a depth of 20 to 30 m near the head. No sign of this tongue was observed on a preceding cruise 5 weeks earlier, and only a trace was evident at Sta. A on the succeeding cruise 5 weeks later. This tongue had dissolved oxygen values as high as 115% saturation, which were probably biological in origin. Three possible mechanisims can be suggested for its development: (1) the tongue could have developed *in situ* as a result of an unusual distribution of the phytoplankton population; (2) the tongue could be a residual maximum resulting from the development of an intense phytoplankton bloom in the top 30 m (this region of high oxygen might later have been cut off from the surface by an inflowing tongue of low-oxygen water from outside the fjord at depths of 10 to 15 m); (3) the tongue could also have resulted from the transport of water from a high-oxygen source of production at the head of the fjord.

The first suggestion is less tenable, primarily because of the intensity of light at 30 m in May, 0.15% of surface light. This is at or below the compensation level for most phytoplankton. It is therefore unlikely that an *in situ* population could produce sufficient oxygen to raise the levels from the observed values of 3.18 to 5.98 mg/l in April to the values approaching 10.0 mg/l observed during May.

The second hypothesis is even less tenable. If one assumes that the inflowing tongue of low-oxygen water intruded into the high-oxygen region just prior to May, the region would probably have had an average oxygen level of about 10.4 mg/l throughout a region 14 km long and 30 m deep. This is a rate of oxygen production exceeding that observed during the bloom in subsurface water in the spring of 1958. Examination of the T–S structure of the water of this region of low oxygen yields no suggestion that this water is of a different origin. The foregoing, combined with the fact that most of the region under discussion is at a depth well below the optimum light intensity, negates this second hypothesis.

The third hypothesis appears to be most likely explanation. Such an area of high oxygen concentration can be seen at Sta. A, where values in excess of 10 mg/l occur at all depths to 30 m. The internal structure of the tongue itself indicates that the highest values occur at the head with decreasing values toward the mouth. This is contrary to the general trend shown by the oxygen distribution in the preceding months, when at all depths from the surface to 50 m there was an increase in oxygen seaward from the head. This decrease was still observed at 50 m during the May cruise. By postulating that the high-oxygen layer flows from the head of the fjord at intermediate depths, the requirement for oxygen production is reduced by about one-third to one-half, placing it just within the possible phytoplankton production during the time available.

However, the possible dynamic mechanism providing such a down-fjord flow is not obvious. The kinematics of the fjord, as represented by the May data, offer no supporting evidence for such a flow. It is possible that the tongue is the residual effect of a flow occurring between the cruises and that it does not continue during May. Whatever mechanism is responsible for the development of this tongue, one must take into account the fact that it is supersaturated with oxygen and is probably biological in origin.

All of the other observed maxima can be traced to the mouth of the fjord. This implies that they result from the inflow of water having different dissolved oxygen characteristics. These maxima occur most frequently during the winter months—usually between October and February.

The highest maximum observed during the three years occurred in January 1957. At this time, the entire southern half of the fjord basin below 50 m was occupied by a mass of water with 7.2 mg/l dissolved oxygen. A similar maximum was observed during December of 1957, when a smaller mass was observed intruding as a tongue at 50 m and extending northward to Sta. C. Again, during February of 1959 a large tongue intruded at 75 m and was traceable northward to Sta. B. All three of these water masses were of sufficient volume to influence the entire length of the fjord at a particular depth.

At other times of the year—usually during the fall months—smaller tongues were observed. One set of these occurred in September through November

1956 at about 50 m. During December 1958, a slight tongue of high-oxygen water dropped into the basin at Sta. F. Examination of the oxygen distribution during the following month shows little residual influence and suggests that the volume of water which intruded was small.

These oxygen distribution patterns suggest that dissolved oxygen, even though it is a non-conservative property, can provide an indication of the circulation pattern of the fjord. This is primarily a consequence of two features. The horizontal distributions of temperature and salinity usually show very small gradients compared with the horizontal distribution of dissolved oxygen. This distribution results in part from the influence that these properties have upon density. Changes in temperature and salinity result in changes in density, and the resulting intra-fjord movement of water seeking its own density confounds the picture. On the other hand, oxygen levels are influenced by biological activity. This is particularly evident when the steady decrease in dissolved oxygen of the relatively undisturbed deep basin waters is considered. The reduction in dissolved oxygen at all depths below the euphotic zone proceeds at a rate much greater than the rate of decrease in density resulting from the downward transport of heat and fresh water. Waters entering the fjord come in at or above the sill depth and therefore usually have a much higher dissolved oxygen content than those of the basin. As a consequence these intrusions show up clearly.

Such intrusions can be noted in two ways. If oceanographic observations are made during an intrusion, the intrusion is apparent as a tongue of high-oxygen water traceable from the mouth of the fjord. If the observations are made shortly after such an intrusion, the intruding tongue is evident (as a detached mass of water with different oxygen characteristics) at some intermediate depth. If the observations are made after the intruding waters have had a chance to mix with the fjord waters, the relative slope of the oxygen isolines reveals the previous intrusion. To illustrate this the following schematic model is presented (Fig. 26). Consider a fjord which has a small horizontal oxygen gradient. In Fig. 26a are shown the isolines prior to the intrusion when they are approximately parallel to the water surface. An intruding mass of high-oxygen water would appear as a tongue replacing the upper isolines (Fig. 26b). Successive vertical mixing of the intruding tongue would develop a pattern of isolines which slopes downward (Fig. 26c). If the intruding tongue were an oxygen minimum, the isolines resulting from vertical mixing would slope upwards from head to mouth. Tidal intrusions would produce a displacement of the isolines roughly proportional to the influence of the mixed intruding waters. A typical pattern resulting from such intrusions is shown in Fig. 26d.

Thus, examination of the oxygen isolines at a particular time can provide at least a qualitative picture of the circulation pattern of the preceding month provided the examination is confined to depths below the euphotic zone, and to times when the outside waters at sill depth show characteristics in their dissolved oxygen content different to those of waters in the fjord basin.

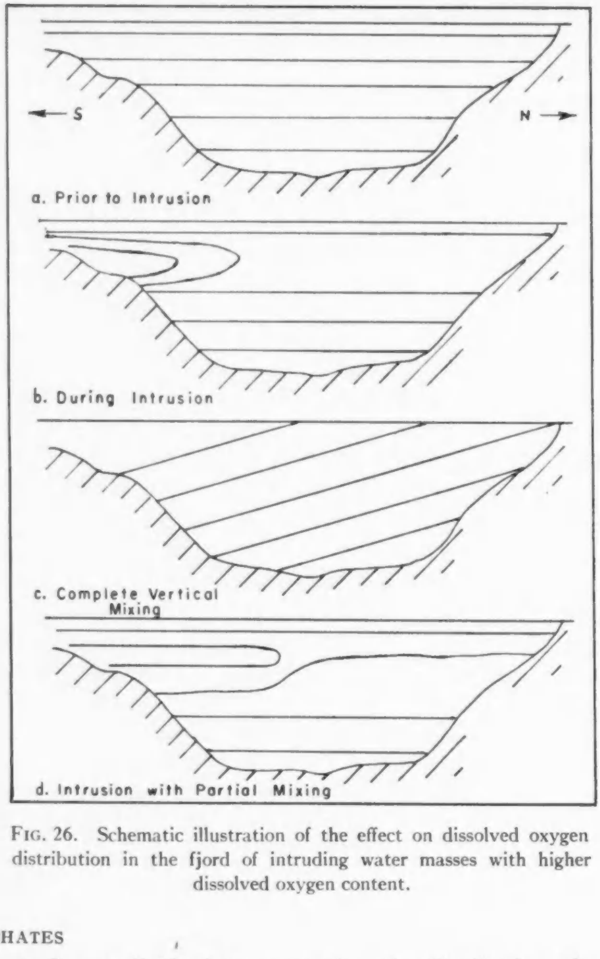


FIG. 26. Schematic illustration of the effect on dissolved oxygen distribution in the fjord of intruding water masses with higher dissolved oxygen content.

4.2. PHOSPHATES

There are few available data concerning the distribution of nutrients in British Columbia fjords. During 1926–1931 some data were gathered at irregular intervals in the Strait of Georgia and several of the southern fjords (*Anon.*, 1931; *Anon.*, 1956; Carter, 1934; Hutchison *et al.*, 1929).

In March 1959, a joint operation with the University of Washington provided the opportunity for a survey of PO_4-P distribution in Indian Arm. The results of this survey, showing both horizontal and vertical gradients, are presented in Fig. 27.

The phosphate concentration of the surface water was 1.89 microgram-atoms (μg-at) P/l at the fjord head and 1.49 near the mouth. This difference, which probably existed in spite of the entrainment of waters with higher phosphate values into the surface layer, results from phosphate utilization by the phytoplankton population. Thus the distribution can be used to obtain an approximation of primary production—if seaward transport and the amount of entrainment are known.

The phosphate contribution of the Indian River can be estimated by considering the relation between the salinity–phosphate values at two depths off the river mouth. In March 1959 the salinity at the surface was 20.26‰ and the phosphate concentration 2.40 μg-at P/l. Figure 27 suggests that inflowing fresh water could mix with underlying water of PO_4-P content as high as 3.0 μg-at P/l. Assuming that this deeper water had salinity 26‰, then theoretically the surface phosphate level should be about 2.3 μg-at P/l, which corresponds very well with observed value. The agreement between the calculated and the observed surface phosphate values suggests that at this season the river contribution is negligible.

The vertical phosphate distribution shows approximately a threefold increase, from a minimum of 1.49 μg-at P/l at the surface to a maximum of 5.29 at 200 m. Since the values at the depth of the sill are estimated to range from 2 to 3 μg-at P/l, it would appear that some concentrating mechanism is increasing the phosphate values in deep water. Such high values in Indian Arm could result from a combination of the following mechanisms:

> a. Fixation of phosphates by phytoplankton in surface waters with their subsequent descent and decomposition of the latter and release of phosphates in deep water.
>
> b. Consumption of the phytoplankton population by herbivorous zooplankton with subsequent phosphate release by decomposition of the animal bodies and their fecal pellets (the rate of this downward transfer of phosphates would be increased if the particular zooplankters exhibited extensive vertical migration).
>
> c. Decomposition of terrestrial organic matter that has sunk to the bottom of the fjord.

These processes would result in a net transport of phosphates from the surface to deep water.

If the water replacement pattern of the fjord results in outside water being introduced at intermediate depths, or if the bottom waters are slowly replaced, the downward transport of phosphates would produce phosphate levels appreciably higher than those at corresponding depths in outside waters. Examination of early (*Anon.*, 1931) data suggest that this may be the case in Indian Arm. The phosphate levels reported for deep basin waters in Indian Arm are approximately three times as large as those at corresponding depths in the Strait of Georgia.

Thus it appears that the organisms within the fjord effectively collect and concentrate the phosphates (and associated inorganic nutrients) of the surface waters in the deep basin. Such a reservoir of nutrients could return to the surface layers during periods of low stability or at times of large inflows into the

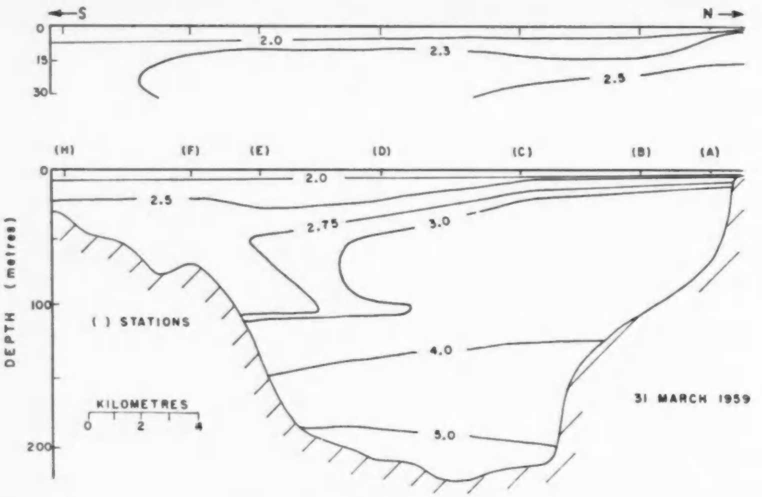


FIG. 27. Distribution of phosphate (μg-atoms P/litre) in longitudinal section through the fjord, March 1959.

deep basin of the fjord. The influx of high-density water would force the nutrient-laden bottom waters up to the surface. It should be noted that this picture is based on data of known reliability from only one cruise in 1959. Since the reliability of the data during the early (*Anon.*, 1931) period is not known, they are not readily comparable.

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NOTES

Temperature and Salinity in the Quoddy Region of the Bay of Fundy[1]

Temperature and salinity data were collected at 14 stations for 43 cruises in the Quoddy Region during 1957 and 1958 (Fig. 1). These were designated "QP Cruises", and were carried out as one phase of the program of the Research Committee of the International Passamaquoddy Fisheries Board in order to assist with prediction of the effects of the proposed tidal power project on the fisheries (Hart and McKernan, 1960).

In addition to the above-mentioned cruises, surveys were made in the Saint Croix and Magaguadavic estuaries in the spring and summer of 1958. Surface salinity samples were taken twice daily at the wharf of the Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B. from December 4, 1957, until December 31, 1958. Surface temperatures have been taken there daily since 1921. Prince Sta. 5 and 6 which correspond with Sta. QP-2 and QP-8 respectively have been occupied monthly for approximately 40 years.

Many other temperature and salinity observations were made during 1957 and 1958 in conjunction with current measurements, drift bottle releases, and herring taggings. The above-mentioned data, combined with the results of observations from numerous surveys of the Quoddy Region over the past 50 years, formed the basis of a manuscript report (Forgeron, MS. 1959). The purpose of this report was to present the temporal and spatial distributions of temperature and salinity, and to infer and evaluate, where possible, the residual flow, flushing time, and controlling oceanographic factors.

In spring and summer, water temperature throughout the Quoddy Region decreases seaward with the maximum temperature of the column found at the surface. In autumn and winter the temperature in general increases seaward with the minimum temperature of the column found at the surface (Fig. 2). The annual temperature curves in the Inner and Outer Quoddy Regions are sinusoidal with an average surface range of 13 and 10 C° and a bottom range of 11 and 9 C° respectively. Temperatures in the Quoddy Region generally reach a maximum in late August or early September and a minimum in late February or early March. In 1957 and 1958 the maximum and minimum monthly mean temperatures recorded for the region were 15.9 and –0.6°C, respectively.

Pyroheliometer records of insolation were collected from April 1957 through December 1958 as part of a heat budget study. A notable feature was the

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[1] International Passamaquoddy Fisheries Board, 1956–59. Scientific Report No. 27.

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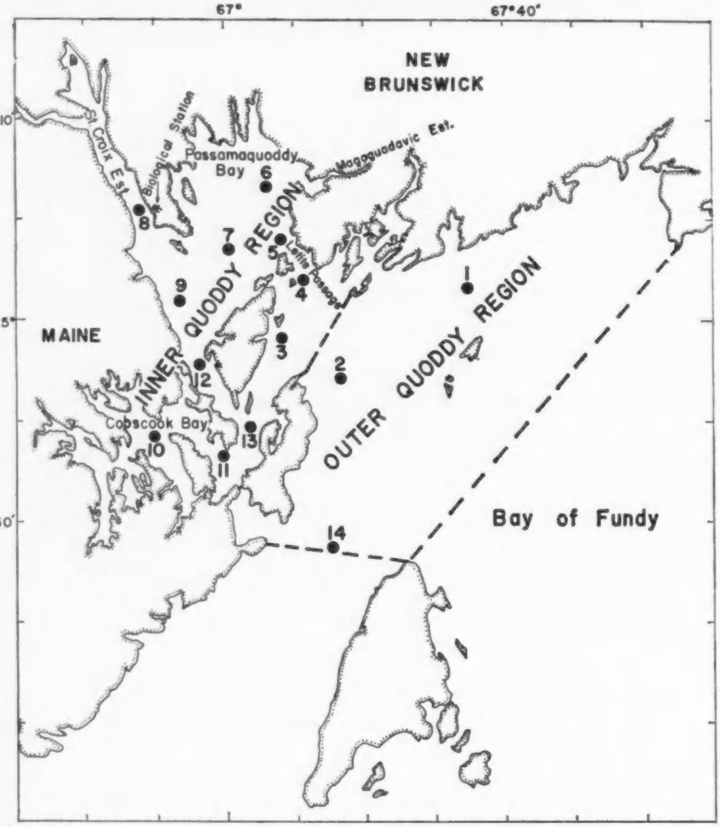
67°
67°40'
45°10'
45°
50'
NEW BRUNSWICK
MAINE
St. Croix Est.
Biological Station
Passamaquoddy Bay
Magaguadavic Est.
Letite Passage
INNER QUODDY REGION
OUTER QUODDY REGION
Cobscook Bay
Bay of Fundy
1
2
3
4
5
6
7
8
9
10
11
12
13
14

FIG. 1. Chart of the Quoddy Region showing station locations.

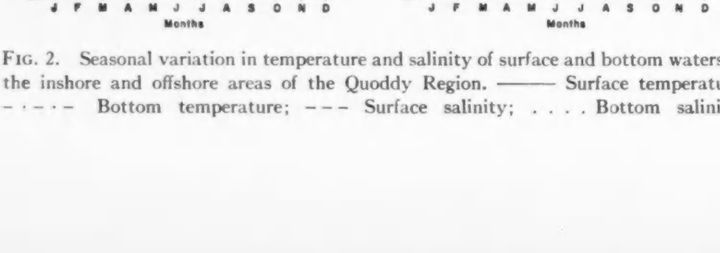

FIG. 2. Seasonal variation in temperature and salinity of surface and bottom waters in the inshore and offshore areas of the Quoddy Region. ——— Surface temperature; – · – · – Bottom temperature; – – – Surface salinity; . . . . Bottom salinity.

markedly higher solar radiation received during the recorded period of 1957 as compared with a similar period in 1958, while the corresponding water temperatures were lower. In addition the water temperatures followed air temperatures more closely than solar insolation. The dissimilarity between curves of water and air temperatures, and that of solar insolation, suggests that the air masses moving through the area are more important in producing abnormal water temperatures than is the local solar radiation.

Salinity in the Quoddy Region increases seaward throughout the year. The average *ranges* of surface and bottom salinities for Sta. QP-8 in the Inner Quoddy Region were 5.7 and 1.5‰, respectively. In the Outer Quoddy Region, at Sta. QP-2, the average annual salinity range at the surface was 1.4‰, and at the bottom, 0.9‰. Salinities in the Quoddy Region generally reach a maximum in October and a minimum in April or May. The maximum and minimum salinities recorded in the Inner Quoddy Region in 1957 and 1958 at QP stations were 32.78 and 21.91‰. In the Outer Quoddy Region the maximum and minimum values recorded were 33.08 and 26.52‰. The ranges of salinities observed in the Quoddy Region in 1957 and 1958 are probably as extreme as are likely to be found because 1957 was a relatively "dry" year and 1958 a relatively "wet" year in terms of fresh water discharged from the rivers.

The difference in temperature between high water and low water varied from near zero in the Outer Quoddy Region to about 0.5 C° in Passamaquoddy Bay. Average salinity *differences* varied from zero in the Outer Quoddy Region to about 3‰ near the heads of estuaries. Generally, between April and October there is an inverse correlation between salinity and temperature changes from high water to low water. For the remainder of the year the temperature and salinity changes occur in the same sense. Throughout the year the lowest salinity over a tidal cycle occurs near low water.

The strong tidal currents create vigorous mixing and provide rapid flushing of the region. Flushing times computed on the basis of the tidal prism and fresh water discharge were found to vary from 8 to 17 days in Passamaquoddy Bay. In the Magaguadavic and St. Croix estuaries flushing times were 2 and 6 to 7 days, respectively.

Significant differences in temperature and salinity between Western and Letite Passages were observed on a seasonal basis. If the mixing processes are similar in both passages it is concluded that residual flow is variable both in direction and magnitude from season-to-season. The wind pattern varies seasonally. It is believed that this contributes significantly in determining the non-tidal surface circulation in the Inner Quoddy Region.

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Predator-Prey Relationships in Pikes (Esocidae)

Association of fishes with other fishes and with other animals is well known from warm seas. The kinds observed vary from the parasitism of *Stegophilus* on armoured catfishes to the symbiotic relationship of *Amphiprion* and anemones, and from the commensal association of *Echeneis* and sharks to the cleaning of parasites from one fish by another. Probably the commonest association between species of fishes is a habitual predator–prey relationship. Predation in this instance is defined in the restricted sense as the pursuit, capture and consumption of one fish by another.

Associations of any type are much rarer in freshwater fishes of temperate areas. Predator–prey relationships are common, but are generally non-specific and choice of prey is dependent on relative abundance only.

Within the pikes (Esocidae) there appears to be a broad range of predator-prey relationships, from those based solely on a critical size relationship between predator and prey, to a more definite association between the two. In the former, choice or selection of prey species appears to depend solely on relative abundance, in the latter some other mechanism may be affecting choice. In the northern pike, *Esox lucius*, according to Allen (1939) and Johnson (1959), perch (*Perca fluviatilis* and *P. flavescens*), trout (*Salmo trutta*) and common sucker (*Catostomus commersoni*) predominated in the diet, but this selection corresponded closely to relative abundance or availability of the prey species. Yellow perch and common suckers were prominant in the diet of muskellunge, *Esox masquinongy*, reported on by Hourston (1952). However, the wide range of fish and other vertebrates consumed made this appear to be selection by size and not by species. Wich and Mullen (1958) recorded that selectivity of food in the chain pickerel, *Esox niger*, was based on relative abundance. Raney (1942) however cited young, easily-caught bullheads (*Ictalurus nebulosus*) as the most frequent prey of chain pickerel in spite of the fact that the number of various species consumed were not in direct proportion to their relative abundance. Common sunfish (*Lepomis gibbosus*) and yellow perch were much more abundant but were preyed on to only a minor extent. Nikolsky (1956) claimed that the food of the Amur pike *Esox reicherti*, consisted of a variety of cyprinids and most often depended on what species was most abundant or what species was migrating through the river at that time.

Evidence of a more definite association has resulted from a study of the biology of *Esox americanus vermiculatus*, the grass pickerel, in Leeds County, Ontario. About 80 collections for grass pickerel were made from various sections of several muddy, narrow, heavily vegetated creeks. Forty-three of these collections yielded both grass pickerel and the central mudminnow, *Umbra limi*. This association appeared to go beyond common habitat requirements since conditions of temperature, depth, vegetation, etc. of many of the locations where none was caught were similar to those yielding both species.

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The mudminnow was, in addition, the principal food of those grass pickerel which feed primarily on fishes (100 mm and over). Of 277 grass pickerel of this size 89 had eaten mudminnows, almost 5 times as many as had eaten the next most frequently eaten fish. A total of 21 other exploitable species of fishes were present in this stream but only 4 species other than the mudminnow were preyed on to any extent. In most collections several species of cyprinids, darters and sunfishes were more abundant than *Umbra limi*.

Once only did it appear that grass pickerel were present without mudminnows. A seine haul contained 4 pickerel and no mudminnows. Other hauls in the same site yielded no more of either species. However, when the grass pickerel were being taken from the net one of them disgorged a mudminnow that had been ingested only very shortly before.

The contrast between the situation described above and that pertaining to two closely related species in North Carolina is interesting. In collecting the redfin pickerel, *Esox a. americanus*, in North Carolina, habitats very similar to those of the grass pickerel were visited. In this area another mudminnow, *Umbra pygmaea*, the eastern mudminnow, occurs. In a total of 11 collections in various streams, sloughs and swamps only 3 localities contained both *Esox a. americanus* and *Umbra pygmaea*. Fourteen species of fishes were present in the stomachs of redfin pickerel but *Umbra pygmaea* was completely absent. In some of the localities from which the redfin pickerel were taken eastern mudminnows were as abundant as centrarchids which were the predominant prey of the redfin.

Thus, in two pairs of closely related esocid fishes living in similar habitats, one pair seem to display a high degree of association and the other pair almost none at all, while other members of the family show a prey selection based principally or solely on relative abundance.

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On the Feeding and Growth of Young Herring (*Clupea harengus* L.) in Captivity

Johnson (1939), Farrin *et al.* (1957), Parrish *et al.* (1958), and Blaxter and Holliday (1958) have reported attempts to keep young herring alive in aquaria, and to study their behaviour, feeding habits and growth while in captivity. An experiment was carried out at the St. Andrews, N.B., station of the Fisheries Research Board of Canada in the summer of 1961 to gain first-hand experience in methods of handling herring in aquaria and to find a diet available in quantity locally that would produce growth. This experiment was preliminary to a proposed study of variations in the behaviour and growth of herring under different environmental conditions.

HOLDING. Three lots of live herring of age groups 1+ and 2+ and from 10 to 18 cm total length were obtained during May and June from weirs in Passamaquoddy Bay. The herring were handled with extreme care to avoid unnecessary loss of scales or injury to the body. At no stage during transportation from the weir to the laboratory tanks were the fish removed from water.

Laboratory holding tanks were made of fibreglass and were 3 different sizes: 6 ft (183 cm) diameter × 4 ft (122 cm) deep; 6 ft (183 cm) diameter × 3 ft (91 cm); and 3 ft diameter × 2 ft (61 cm). They were filled to 44 inches (112 cm), 31 inches (79 cm) and 20 inches (51 cm), respectively, and then contained approximately 650, 450 and 75 imperial gallons (2,960, 2050 and 340 litres). The tanks were gravity fed with sea water from a storage tank and were equipped with air-stones. To assure circulation at all depths in each tank, the inflowing water was passed through a vertical "Uscollite" plastic tube $\frac{3}{4}$ inch (19 mm) in diameter, with perforations spaced 6 inches (15 cm) apart. High rates of water and air inflow were found to be disturbing to the fish, especially during the early days of captivity when they passed through a period of starvation and almost continuous flight reaction. As a result, the inflow of water and air, although not measured, was maintained at moderate to low levels throughout the experiment.

About 600 to 700 fish were placed in each of two 650-gallon tanks and about 100 in each of two 75-gallon tanks. During the first few days the mortality rate was high in all tanks. However, this gradually decreased as the fish became accustomed to the new environment and commenced feeding on the small amounts of food that were dropped into the tanks at least three times daily. Feeding commenced in the large tanks on the 12th to 14th day and in the small tanks on the 30th day. However, feeding in the small tanks was sporadic and

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they were therefore abandoned. After the fish had commenced feeding in the large tanks, about 150 to 200 were transferred to a 450-gallon tank. Feeding continued at a high level in this tank for some days then eventually dropped and it too was abandoned.

All holding tanks were cleaned frequently by siphoning out the unused food and other debris. A clean tank seemed to encourage feeding and to decrease the mortality rate. On a cloudy day the herring fed better with artificial illumination from above.

FEEDING. Herring were fed the following diets and were given all they would eat at a feeding:

1. A finely-ground mixture of sea mussels and equal parts of "Puss and Boots" cat food with small quantities of terramycin and yeast extract. Farrin *et al.* (1957) maintained herring successfully for two years with this formula but didn't report any growth. In the present experiment, using a near-freezing mixture, the food particles disintegrated rapidly and the fish were able to take only small quantities.

2. A mixture of "Purina Chow Pellets" (poultry feed) and herring in equal proportion. This mixture was frozen and presented to the herring as small flakes. Flaking increased the buoyancy of the food particles and made them much easier for the herring to take in quantity. Once the fish had commenced feeding much of the food dropped into the tank was eaten eagerly. Frequently the fish took food particles at the surface and occasionally from the hand.

3. Chopped squid. Blaxter and Holliday (1958) found that herring took chopped squid readily and grew 2–3 cm and 20–30 g in 9 months. Present experiments confirmed that herring would eat chopped squid and indicated that they favoured small, rectangular pieces about 4 × 3 mm in size. This food was also fairly buoyant and provided a good opportunity for feeding. The difficulty in obtaining squid prevented testing for a long period.

4. Small pieces of herring. Small, dead herring, available in quantity locally, were kept for about 10 days at 0°C. This resulted in partial softening or breakdown of the flesh which was then fed in small pieces to the captive herring. The herring appeared to prefer this type of food over any of the other three diets. This is contrary to the results of Blaxter and Holliday (1958) who reported that captive herring preferred chopped squid to small pieces of herring.

GROWTH. Associated with the study of feeding, the growth rate of herring was observed from June to September in one of the 650-gallon tanks containing 500 to 600 fish. Four samples of fish were taken during the period. Length measurements were made to the nearest millimetre to the tip of the longer lobe of the tail, when directed straight back.

Water temperatures inside the tank ranged from 9.0 to 14.3°C. The fish were fed twice daily with about 500 g of herring flesh. During feeding there was little or no competition among fish of the same size and there appeared to be no size hierarchy.

Table I shows that during the first 42 days of the experiment the increase in mean body length was only 0.4 cm. This small amount of growth can be attributed to the fact that the fish passed through a period of starvation during that time. During the whole 89-day period, however, mean length increased by 3.0 cm. The table shows that there was a decrease in growth rate between mid August and mid September. This was probably the result of an observed decrease in food intake during early September. During the same period there was a significant rise in the water temperature, which was not controlled during the experiment.

TABLE I. Growth of herring in captivity, 1961.

Date	Period	Water temp.	No. of fish	Total length		Instantaneous growth rate*
				Range	Mean	
	days	°C		*cm*	*cm*	%
June 15	0	9.0	100	11.7–17.5	13.6	...
July 27	42	9.0–12.0	102	12.5–18.0	14.0	0.069
Aug. 14	18	12.0–12.5	55	13.5–18.6	15.1	0.420
Sept. 12	29	12.5–14.3	100	14.3–20.0	16.6	0.327

*Calculated using formula $\frac{\log_e L_2 - \log_e L_1}{t}$, from Simpson and Roe (1939).

The increase in mean length (3.0 cm) is similar to that reported by Blaxter and Holliday (1958) for slightly larger fish (16–22 cm) but it occurred over a much shorter period (3 months, as compared with 9 months). It is also worthy of note that samples of herring from commercial herring catches in Passamaquoddy Bay in 1961 showed an increase in mean length from 14.5 cm in mid June to 17.9 cm in mid September. Thus, the growth of herring in captivity was only slightly less than the growth in nature.

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A Relationship Between Growth, Hatching and Spawning Season in Canadian Atlantic Herring (*Clupea harengus* L.)

Spring and autumn spawning herring support separate fisheries in Chaleur Bay, Gulf of St. Lawrence, and are part of the same unit stock (Jean, 1956).

Herring were sampled in 1960 and 1961 from the spring and autumn fisheries in Chaleur Bay. Following techniques developed by Einarsson (1951) and Parrish and Sharman (1958, 1959), otoliths were used to determine the hatching season of the fish, and the amount of 1st-year growth. A domed opaque nucleus indicated spring hatching and a depressed hyaline nucleus autumn hatching. Using a micrometer eyepiece, the size of the 1st-growth zone on the otolith was measured from the centre of the nucleus to the outer edge of the 1st-winter ring at the post rostrum (Fig. 1). The measurement was recorded in eyepiece units (1 eyepiece unit = 0.043 mm).

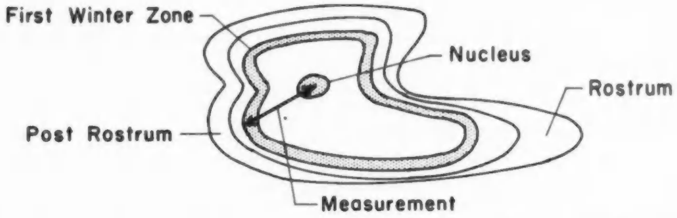

FIG. 1. Drawing of a herring otolith showing the location of the 1st-growth zone.

Table I shows that spring-hatched fish dominated the spring fisheries of 1960 and 1961, and the autumn fishery of 1961.

Table II shows that, in both fisheries in 1960 and 1961, the 1st-growth zones of otoliths of autumn-hatched fish have a greater mean size than spring-hatched fish. This is probably because autumn-hatched fish do not produce a ring on the otoliths during their first winter. The zone size difference supports the use of the appearance of the otolith nucleus to determine hatching season.

Statistical tests on the data in Table II showed that, within the fisheries in both years, there was little significant difference in 1st-year growth between spring- and autumn-hatched fish ($d = 1.1571$, $P > 0.10$). However, between fisheries in both years, this difference was highly significant ($d = 3.874$, $P < 0.001$). Thus, both the spring- and autumn-hatched fish in the autumn fisheries have significantly greater 1st-year growth than do those found in the spring fisheries.

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TABLE I. The relationship between growth, hatching and spawning season, and landings of Chaleur Bay spring- and autumn-spawning herring. Number of fish in brackets. Landings are those of the peak months in Fisheries Statistical District #65, Gloucester County, New Brunswick, in millions of pounds (10^6lb = 454 metric tons). 1952 data are from Jean (1956), adapted as described in the text.

Year	Mean length for age 7	Spring hatched	Autumn hatched	Landings
		Spring-spawning fishery		
	cm	%	%	*10^6lb*
1952	31.3 (136)	87 (4873)	13 (728)	6
1960	33.3 (83)	58 (289)	42 (210)	3
1961	32.0 (73)	73 (361)	27 (134)	⅓
		Autumn-spawning fishery		
1952	33.4 (13)	52 (717)	48 (662)	1
1960	33.7 (37)	45 (89)	55 (109)	2
1961	34.6 (57)	57 (256)	43 (196)	2

The autumn spawners have a higher growth rate than the spring spawners (Jean, 1956; Tibbo, 1957). Jean found that autumn spawners have larger 1st-year growth zones on the scales, and suggested that the rate of growth of the fish in its first year may determine the season in which it spawns.

The significantly larger 1st-growth zones of otoliths of autumn-spawning fish in 1960 and 1961 (Table II) provides further evidence for the above suggestion.

The greater length of the autumn spawning fish, as shown in Table II, suggests that this trend in 1st-year growth is maintained to maturity, i.e., at age 3 or 4 in Chaleur Bay herring (Tibbo, 1957).

For the majority of herring, spring hatching leads to spring spawning and autumn hatching to autumn spawning (Table I). The remaining proportions are presumably made up of fast-growing, spring-hatched fish which become autumn spawners, and slow-growing, autumn-hatched fish which become spring spawners.

TABLE II. Mean size of 1st-year growth zones of otoliths from spring- and autumn-hatched herring taken in the spring and autumn fisheries for spawning herring in Chaleur Bay, 1960–61.

	Spring fishery		Autumn fishery	
	Range	Mean	Range	Mean
1960	*mm*	*mm*	*mm*	*mm*
Spring-hatched	0.65–1.08	0.90	0.86–1.29	1.08
Autumn-hatched	0.77–1.20	0.99	0.86–1.33	1.12
1961				
Spring-hatched	0.60–1.08	0.82	0.47–1.42	1.03
Autumn-hatched	0.69–1.20	0.90	0.65–1.55	1.08

Jean (1956) showed that the spring-spawning stock in 1952 was composed of approximately 52% spring-hatched, 40% intermediate, and at least 8% autumn-hatched. For comparison with 1960 and 1961 figures it was considered justifiable to assign the intermediates proportionally to the spring- and autumn-hatched percentages yielding a ratio of 87% spring-hatched to 13% autumn-hatched.

Figures presented in Table I and including the period 1960–61 indicate that, since 1952, autumn-hatched fish have become more abundant; and mean length for age 7, a representative age group, has increased.

Table I shows that in the spring fishery the mean length at age 7 and the percentage of autumn-hatched herring fluctuated in direct proportion. Generally, after 1952 the proportion of autumn-hatched fish increased and landings decreased in the spring fishery. In the autumn fishery growth increased, the proportion of autumn-hatched fish showed no definite trend and landings increased.

Thus, here is strong evidence that the season at which these fish spawn, is not necessarily the same as the hatching season, and is influenced or determined by the rate of growth in the first year, as shown by scales and otoliths. An increase in the relative amount of autumn-hatching and spawning has taken place, and mean length has also increased. Therefore, there appears to be a definite relationship between growth, hatching and spawning season in the Chaleur Bay herring stock.

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